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## Phylogeny and Classification of the Aculeate Hymenoptera, With Special Reference to Mutillidae

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# Phylogeny and Classification of the Aculeate Hymenoptera, With Special Reference to Mutillidae<sup>1</sup>

DENIS J. BROTHERS<sup>2</sup>

## ABSTRACT

The phylogeny (and classification) of the aculeate Hymenoptera has not been examined as a whole since Börner's limited study of the entire Hymenoptera 55 years ago. The relationships of the members of the "Scolioidea," especially the tiphoid-mutillid complex, have been especially confused. This investigation attempts to rectify this situation.

Representatives of 25 taxa of aculeate Hymenoptera (the taxa varying in categorical level from tribe to superfamily in a traditional classification, the emphasis being on the "Scolioidea") were examined with respect to 92 characters. Primitive-derived sequences of states were determined for these characters and cladograms were constructed by electronic computer ("Wagner trees") and by hand using the principles of Hennig. The most variable characters were eliminated and cladogram construction was repeated until similar cladograms were derived by both methods. All derived states of all characters were inserted on the cladogram and numerical measures of distinctness, considering the number of derived states per internode, the number of species subtended by (i.e., resulting from) each internode and the efficiency (in terms of unique, parallel or convergent occurrences) of each derived state on each internode, were calculated. Taxonomic distinctness of each taxon from every other was calculated, and this measure was used as a guide in establishing the categorical levels to which the taxa were assigned in a classification.

Representatives of 89% of the valid described genera and subgenera of myrmosids and mutillids were examined and cladograms were derived as for the Aculeata. The final cladogram of the mutillid-myrmosid group was based on 43 characters (involving 61 derived states), 20 of females and 23 of males. Distinctness measures were calculated, based on these characters only.

These investigations suggest that the aculeate Hymenoptera comprise three superfamilies, each with numerous families: 1. Bethyloidea, containing Plumariidae, Bethylidae, Scelebythidae, Cleptidae, Chrysididae, Loboscelidiidae, Dryinidae, Sclerogibbidae and Embolemidae; 2. Sphecoidea, containing two informal groups, one (Spheciformes) consisting of Ampulicidae, Sphecidae, Larridae, Mellinidae, Pemphredonidae, Astatidae, Philanthidae and Nyssonidae, and the other (Apiformes) consisting of Colletidae, Halictidae, Oxaeidae, Andrenidae, Melittidae, Fideliidae, Megachilidae, Anthophoridae and Apidae; and 3. Vespoidea, containing two informal groups, one (Vespiformes) consisting of Tiphidae, Sapygidae, Mutillidae, Sierolomorphidae, Rhopalosomatidae, Pompilidae, Bradynobaenidae, Scolidae, Masaridae, Eumenidae and Vespidae, and the other (Formiciformes) consisting of Formicidae only.

The composition of most families of Vespoidea is unchanged, but the Tiphidae consists of only the subfamilies Anthoboscinae, Thynninae, Myzininae, Methochinae, Tiphinae and Brachycistidinae. The Bradynobaeninae, with Typhoctinae (including Eotillini), Chyphotinae and Apterogyninae, is placed in the family Bradynobaenidae. The Mutillidae consists of seven subfamilies: Myrmosinae, Pseudophotopsidinae, Ticoplineae, Rhopalomutillinae, Sphaerophthalmiinae (comprising two tribes, Dasyabrini and Sphaerophthalmiini, the latter with the subtribes

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Pseudomethocina and Sphaerophthalmina), Myrmillinae and Mutillinae (comprising two tribes, Mutillini and Ephutini, the former with the subtribes Mutillina and Smicromyrmina).

The cladogram of the Mutillidae and the geographic distributions of its component taxa suggest that the family arose on Laurasia and differentiated in northeastern Africa. The New World members were possibly derived almost entirely from two independent stocks introduced to South America from Africa, and the Australasian fauna probably resulted in the main from a few introductions from South America across Antarctica.

## INTRODUCTION

The Hymenoptera is a well-defined order of endopterygote insects, often considered to comprise a distinct superorder (e.g., Mackerras, 1970), and is undoubtedly holophyletic (Ashlock, 1971, 1972; = monophyletic *sensu* Hennig, 1966a). Within the Hymenoptera, the suborder Apocrita (= Clistogastra) is also holophyletic, being characterized by development of a constriction between the first and second abdominal segments and fusion of the first abdominal segment with the thorax to form the propodeum. This situation is unique in the Insecta. (Because of these morphological modifications, the tagmata of apocritans are referred to below as "head," "mesosoma," and "metasoma," for the head, apparent thorax and apparent abdomen, following the suggestion of Michener, 1944.) By contrast, the Symphyta (= Chalastogastra) is almost certainly a paraphyletic group (*sensu* Ashlock, 1971, 1972; not Nelson, 1971) as Rasnitsyn (1969: p. 168, Fig. 273) has demonstrated, the Apocrita possibly having been derived from within the Siricoidea.

Although the Apocrita is often formally considered to comprise a number of equivalent superfamilies (e.g., Riek, 1970), an informal division into two groups is useful. One of these groups, the Aculeata, is holophyletic, being characterized mainly by modification of the ovipositor as a stinging apparatus (see Oeser, 1961, for various characters involved). The other group, the Terebrantia (= Parasitica) is undoubtedly paraphyletic, comprising the

remaining apocritans. Richards (1956b) considers these groups more formally as sections.

The Aculeata is commonly considered to comprise seven superfamilies ("Bethyloidea," "Scolioidea," "Pompiloidea," "Formicoidea," "Vespoidea," "Sphecoidea" and "Apoidea") of which the first two are judged to be the most primitive in general (e.g., Evans & West Eberhard, 1970). (Since this study has led to conclusions which involve changes in the limits of taxa previously recognized at the family and superfamily levels, names used in the old sense are enclosed in quotation marks throughout.) Most of these superfamilies are readily characterized by one or more unique specializations and thus are clearly holophyletic. The "Scolioidea" is an exception, however, since this group appears to contain those aculeates which do not clearly fall into any of the other superfamilies. It is thus probably paraphyletic or even polyphyletic (*sensu* Hennig, 1966a; Ashlock, 1971, 1972; not Nelson, 1971), although shown as holophyletic in the dendrogram of Evans & West Eberhard (1970). The "Scolioidea" further contains various taxa the placement of which has been confused. The main purpose of this investigation is thus the clarification of the interrelationships of the various taxa comprising the "Scolioidea," with special emphasis on the "Mutillidae," and the derivation of a classification which reflects these interrelationships adequately. Coincidentally, the study has been extended to cover the entire Aculeata.

There have been widely differing clas-

sifications at the higher levels for the members of the scolioid complex, notably the "Tiphiiidae" (*sensu lato*). Thus, de Saussure (1892) considered the entire complex to be a single family (*Hétérogynes*) and Ashmead (1900, 1903-1904) differentiated eight families in this group. Pate (1947a) provided some clarification of the genera related to *Tiphia*, *Myzinum*, etc., and Krombein (1951) included six families in the "Scolioidea" of North America. Tobias (1965) elevated one of these families ("Sapygidae") to the superfamily level so that he could designate its two subordinate taxa as families. The "Mutillidae" has consistently been considered an important member of the "Scolioidea."

The "Mutillidae" is a large, cosmopolitan group of wasps, the classification of which has also long been in a state of confusion. The group included by Linnaeus (1758) and other early workers in the genus *Mutilla* was much broader than the present family "Mutillidae." (The following outline excludes those sections more recently considered to fall in other families.) Although there were preliminary attempts by workers such as Latreille (1809, 1825, 1829), Wesmael (1851), Sichel & Radoszkovsky (1869), Thomson (1870), Blake (1871, 1886), Burmeister (1874) and de Saussure (1892) to develop a higher level classification within the group (often by merely describing a few new genera or subgenera for species which were superficially aberrant), subsequent workers such as Fox (1899, 1900) again reduced most genera to synonymy of *Mutilla*, although suggesting species groups within the genus. However, André (1899-1903, 1902) and Ashmead (1900, 1903-4) described many new genera and each proposed a different classification for the group. The differences between the two schemes resulted mainly from tendencies by André to lump many taxa into a single family (Mutillidae), while Ashmead placed the

equivalent taxa in four families (Cosilidae, Thynnidae, Myrmosidae and Mutillidae). Bischoff (1920-21) based his classification of African species mainly on that of André (1902), with the addition of various tribal divisions and taking into account Börner's (1919) phylogeny of the Hymenoptera. Bradley & Bequaert (1923, 1928) formulated a scheme that combined features of those of André (1902) and Ashmead (1900, 1903-4). Concurrently they placed most members of two of Bischoff's tribes (Trogaspidiini and Smicromyrmini) in a single genus (*Smicromyrme*). Skorikov (1935) proposed a classification which essentially raised the previously recognized taxa by one categorical step, placing the two tribes of Bischoff in question as subfamilies. Schuster (1947, 1949) recognized that previous attempts at a classification of the group had often been rendered inapplicable because they had been based on too limited material. He proposed a scheme which attempted to take this into account even though he apparently saw few specimens from the Old World. This scheme was adopted by Krombein (1951) for Nearctic species. By contrast, Invrea (1964) used a classification essentially based only on Old World species for the Italian fauna, thus perpetuating the type of arrangement that Schuster had attempted to eliminate.

The present study was initiated as an attempt to derive a broadly applicable classification of the "Mutillidae" from consideration of the entire world fauna (specimens were available for approximately 90 percent of the described taxa at the genus level). After initial investigations it became apparent that the "Mutillidae" as previously delineated was almost certainly polyphyletic, as had been suggested by Schuster (1949). As a result, the investigation was extended to other members of the "Scolioidea" in an attempt to find the smallest holophyletic group upon which a

classification could be based. The superfamily "Scolioidea" proved to be at most paraphyletic (as suggested above), so that the remaining divisions were added to the investigation.

Although the study was thus broadened to include the entire Aculeata, the levels of accuracy and completeness vary considerably, depending on the problem being investigated at each stage. Thus the study of the "Mutillidae" and closely related groups is the most complete and hopefully the most accurate. As higher and higher level taxa were added into the study, time and logistics militated against each being considered as completely as were the taxa originally investigated. Further inaccuracies may have been caused by the unavailability of specimens of rare groups, resulting in the absence of data for some characters of these. The unavoidable inaccuracies introduced at the higher levels as a result of these factors are, however, of minor importance for the main focus of the study, viz., the relationships of the "Mutillidae."

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## METHODS

The methods by which the final cladistic diagrams were derived were essentially the same no matter which taxonomic grouping was involved. First, the operational taxonomic units (OTU's) under consideration were surveyed in an attempt

to discover as many differentiating character states as possible. Each character was re-examined to ensure that the different states could be unambiguously recognized and placed in a coded sequence of "primitive" (or ancestral) to "derived." If there was much uncertainty, the character was rejected. Then, using the selection of least equivocal characters remaining, a cladistic dendrogram was constructed, using two methods. First, a diagram was constructed by hand using the principles of Hennig (1966a) as elaborated by Brundin (1966) and others, i.e., basing all groups on common possession of the derived state of one or more characters (synapomorphies). Second, a diagram was derived by use of a computer program for construction of "Wagner trees" (Farris, 1970; Kluge & Farris, 1969). The hand- and machine-derived trees, representing different approaches to the problem (Moss & Hendrickson, 1973), were then compared. All characters were re-examined in the light of their distribution on the trees and those characters which showed many separate derivations or reversals of the same state were eliminated because of their instability. Certain characters were found to be in need of re-coding, either because of inappropriate delimitation of states or misinterpretation of the primitive-derived sequence. Judgments were based on the principle that most parsimonious placement of states on the trees was the most likely to be correct, unless logically contraindicated (e.g., a most parsimonious placement requiring the re-appearance of a complex structure in an identical form after being lost). During the process of consideration and rejection or retention of characters, due importance was given to the complexity of the character concerned. Thus, for example, a character involving a complex of morphological features was considered to be less likely to have undergone multiple independent changes to a

similar derived state than was a simple character involving a single structure. During the examination process various additional characters were discovered and incorporated into the data matrix.

Once all the characters had been re-evaluated, cladistic diagrams were again constructed by hand and using the computer. These were again compared, the characters re-evaluated and new characters added, etc. This process was repeated until highly similar or identical cladograms were derived using the two methods of construction, indicating that the characters used presented a distribution of derived states that were meaningfully correlated. This final scheme (or highly similar schemes) also most likely embodied the maximal number of "uniquely derived character [states]" and the lowest "coefficient of character-state randomness" (Le Quesne, 1969, 1972) possible.

The initial studies were done using selected genera traditionally included in the "Mutillidae" (*sensu* Schuster, 1947, 1949) as well as representatives of the various subordinate taxa considered to comprise the "Tiphidae" (*sensu* Pate, 1947a), the family thought to be most closely related to the "Mutillidae." These investigations led to two independent lines of study, viz., relationships between the Mutillidae (*sensu stricto*) (the characteristics of which had been established by the initial study) and other taxa within the traditional "Scolioidea" and eventually the Aculeata (taxa being added at higher and higher levels as the study progressed), and the relationships within the Mutillidae.

For the studies involving the Aculeata the characteristics for the various taxa were derived from relatively few species chosen to cover the variation within the taxon as completely as possible, but with emphasis on the presumably least specialized forms. The categorical levels of the

taxa involved varied from tribe (in the "Mutillidae") to family (for most other "Scolioidea") or superfamily (for the non-scolioid aculeates). The material examined in each instance is listed in the account of the primitive characters of each taxon, below.

The general usefulness of any classification depends on the purposes for which it was drawn up. In the present study the attempt has been made to formulate a classification of as general applicability as possible. A classification appears to be of broadest use when it is based neither exclusively on raw phenetic data divorced from any consideration of evolutionary pathways ("pure phenetics," as advocated by Sneath & Sokal, 1973, and others) nor derived from a rigid insistence upon strictly holophyletic taxa, paraphyletic groups being inadmissible ("pure cladistics," as proposed by Hennig, 1966a, 1969, necessitating a complex numbering system; and others), but considers both these aspects, as well as chronistic information (which is present in a relative sense in any cladogram), and may be termed "natural."

Such a classification may be based on a cladogram, with the limits and ranks of the included taxa being delineated by phenetic considerations. Sneath & Sokal (1973) consider that "basing taxonomy on all three approaches [i.e., phenetics, cladistics and chronistics] requires art or compromise, both of which are inadmissible as bases for a precise science." The present study is an attempt to achieve the ideal by minimizing this "requirement," as has been called for by Hull (1970).

As Tuomikoski (1967) and Ashlock (1971, 1972) have pointed out, paraphyletic groups fulfill the basic requirements of monophyly which have always been regarded as essential properties of good taxa. There is thus no reason to discard taxa which are found to be paraphyletic if they are phenetically about as homogeneous as



are holophyletic taxa at the same categorical level. On the other hand, a classification including paraphyletic taxa should not be used as the basis for studies (e.g., zoogeography) which require accurate knowledge of branching patterns displayed in the cladogram from which the classification was derived. (The numerical methods used to obtain indices of phenetic distinctness for the various groups in a cladogram are discussed below, in the section on "derivation of a classification" for the Aculeata.)

Previous classifications and evolutionary schemes of the higher Hymenoptera have generally not been based on strict consideration of synapomorphies. This defect was encouraged by the presence of trends which appear in various lines apparently independently but are characteristic of many of the more derived groups. For example, there is a general tendency toward reduction of the degree of articulation between the various mesosomal sclerites, especially in the pleural region, expressed in various ways in the higher Aculeata. The consideration of such trends as being characteristic of a single line has been responsible for the conventional (inadequate) view involving sequential divergence of various taxa from a single evolutionary line (e.g., the scheme provided by Evans & West Eberhard, 1970).

A detailed study of the hymenopteran ovipositor by Oeser (1961) has, however, used Hennigian principles in the derivation of a very limited cladogram which demonstrates that the Aculeata in the broad sense are holophyletic [females have lost the cerci, section I of the gonocoxite IX is dorsoventrally constricted, and the basal portion of the "notum" of gonapophysis IX is detached (terminology of Smith, 1970a & b); all three are derived states occurring in the Aculeata only], as are its two component sister groups, the

"Bethyloidea" and the remaining Aculeata (*sensu stricto*). This study, admittedly based on a limited suite of characters albeit ones involved in a structural system of great complexity, has provided the rationale for restricting the present study to the Aculeata. Comparisons were also made to the Trigonalidae (Terebrantia) since these have been considered representative of the possible ancestors of the Aculeata (Lanham, 1951; Riek, 1970). Decisions as to the direction and course of evolution of some characters were also aided by reference to a few members of the Symphyta (Argidae, Cimbicidae, Diprionidae, Siricidae, Tenthredinidae, Xyelidae) and Terebrantia (Braconidae, Chalcididae, Gasteruptiidae, Ibaliidae, Ichneumonidae).

## INVESTIGATION OF THE ACULEATA

### States of the Characters Considered

The characters used in the analysis of the Aculeata vary greatly in scope and plasticity. Some characters are uniform in all taxa examined except for a single taxon, these representing unique evolutionary innovations serving to differentiate only the taxon bearing the derived state. Such autapomorphies do not associate taxa and are of minor phylogenetic significance. They do, however, contribute to the phenetic component of the degree of differentiation of the taxon in question from its sister group. In such cases it is usually relatively easy to decide which state is primitive and which is derived; the more common state is primitive. Other characters present synapomorphies which serve to associate two or more taxa on a common branch of the cladogram by virtue of their sharing the uniquely derived state of the character. The direction of evolution in such characters may sometimes not be obvious and must then be determined with reference to the states in forms pre-

sumed to be generally more primitive than the Aculeata. The degree of congruence with the patterns of derivations presented by other characters is also significant.

Some states that are seemingly synapomorphic may not represent unique derivations; a superficially similar derived state may occur in more than one location on the cladogram but in remote sections of it (resulting in convergences). Such a situation reduces the usefulness of the character to some extent. Other characters show tendencies toward the evolution of similar derived states numerous times, often in the same general section of the cladogram, expressed as parallelisms. Although such plastic characters are mostly of minor use in associating taxa on particular branches, they are often useful in indicating which of two taxa associated on the basis of other characters may be considered the more highly derived. In such cases the character involves the "tendency toward" a particular derived state. If formulated in this way the derived state may be envisioned as having evolved (in some preliminary but unexpressed fashion) some time before its appearance on any of the branches of the cladogram, perhaps as the result of accumulated muta-

tions in a non-functional set of gene loci producing a "frozen accident" (see Ohno, 1973).

The numbering system for character states reflects the pattern of evolution for the character involved. Each subsequent digit, reading from the left, refers to a state derived from that expressed by the digits preceding it. This is illustrated in Fig. 1, which shows the pattern of evolution of character 21. Where a particular derived state is characteristic of an entire taxon it is referred to below as being present "in" the group concerned. If a derived state is found in only some members of a taxon and is not characteristic of the entire taxon, it is referred to as occurring "within" the group involved. Placement of the various derived states on "internodes" refers to the final cladogram (Fig. 2). Where examples are given below, the use of a genus name does not necessarily imply that all members of the genus show that character state, but that one or more species do; nor are examples of groups containing a few members with a particular state meant to encompass all such groups. The ending "-id" also does not imply family status.

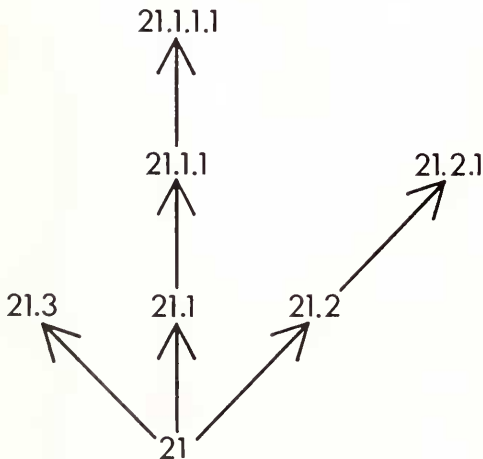


FIG. 1. Diagram of evolution of character 21, showing scheme for numbering the states.

Although it is inappropriate to refer to taxa as being "primitive" or "advanced," since each taxon exhibits characters in both the "primitive" and "advanced" (or "derived") states, it is convenient to refer to taxa in this way on occasion. When a taxon is referred to as being "primitive" this generally means that it originates low on the cladogram and bears relatively few characters in derived states.

Those characters considered to be most useful in the final construction of the cladogram are marked with an asterisk (\*). Even in these, all derived states are usually not equally useful and in some instances one state is practically of no significance whereas another is of great importance.



Certain characters were confirmed or derived from studies by Reid (1941) on the mesosoma, Snodgrass (1941) on the male genitalia and Oeser (1961) on the female genitalia. Genitalic terminology is that of Smith (1969, 1970a & b). Wing venation is based on the terminology of Hamilton (1971, 1972a & b), derived from that of Ross (1936). The number of closed cells includes the costal cell if that cell is present and closed. The symbols used for the behavioral formulae are based on those of Iwata (1942, 1950) as used by Evans (1966b) but with some modifications, mainly those necessary to include the bees in the same scheme. The symbols are as follows: Preparation of next = I (*instruere*); Searching for larval provisions = V (*venari*); Transport of provisions = T (*transferre*); Preparation of provisions—paralysis of animal prey = P (*pungere*), preparation (often "mixing") of pollen-nectar mass = M (*miscere*); Oviposition = O (*ovum parere*); Final closure = C (*claudere*); Provisions—of animal origin = subscript *a*, of vegetable origin = subscript *v*. Other terminology is explained where necessary in the section on the character involved, below.

\*1. *Sexual dimorphism, general form.* Primitively, sexual dimorphism in general body form is minimal except that the male may be slightly smaller than the female and sometimes members of one sex may be apterous. 1.1—The male is considerably more slender than the female and is very elongate, thus being of quite different form.

No or only slight sexual dimorphism is considered primitive because this is the condition in most non-aculeate Hymenoptera and also in most members of the Aculeata.

State 1.1 is uniquely derived, occurring on internode 12-13 and forming a synapomorphy which links the myzinid and methochid groups. However, *Pterombrus*

(myzinid) has the general sexual dimorphism only slight, indicating that state 1.1 may have been reversed within the myzinid group, or it may have arisen within the myzinid group. There is actually a tendency toward increased slenderness in the males within the entire branch subtended by internode 7-10 except for the tiphid and brachycistidid groups, but its development to a very similar extreme in the myzinid and methochid groups leads to male slenderness being placed as above. Further, some members of the scoliid (e.g., *Campsomeris*) and apid (e.g., *Corynura*; Eickwort, 1969) groups have moderately slender males, but these are not of the same form as those included in the groups possessing state 1.1.

2. *Sexual dimorphism, aptery.* Primitively, both sexes are fully winged, or, rarely, both sexes have the wings equally reduced. 2.1—Sexual dimorphism is considerable, with the male winged and the female apterous.

No sexual dimorphism in wing development is considered primitive because this is the condition in most non-aculeate Hymenoptera and also in most aculeates.

Aptery in the female only has occurred on numerous occasions independently throughout the Aculeata. State 2.1 has developed on internodes 8-9 (associating the myrmosid and mutillid groups) and 18-21 (where it links five taxa), and in the plumariid, thynnid, methochid and brachycistidid groups. In view of its sporadic occurrence, little weight should be attached to it even where it does indicate synapomorphy. Furthermore, female aptery (or brachyptery) has arisen within the bethylid (e.g., *Deinodryinus*, *Pristocera*; Evans, 1964a), myzinid (e.g., *Braunsomeria*), tiphid (e.g., *Pseudotiphia*; Nagy, 1969b) and formicid (all workers, some queens, e.g., *Dorylus*, *Eciton*; Wilson, 1971) groups. [Aptery or brachyptery in both sexes has arisen within the

rhopalosomatid (e.g., *Olixon*) group; brachyptery in males only occurs within the apids (e.g., *Lasioglossum*; Houston, 1970; *Perdita*; Rozen, pers. comm.).]

3. *Sterile caste*. Primitively, all female individuals are capable of reproduction. 3.1—There is a specialized caste of females with reduced or no reproductive capability.

The lack of a sterile female caste is considered primitive because this is the condition in all non-aculeates and the vast majority of aculeate Hymenoptera.

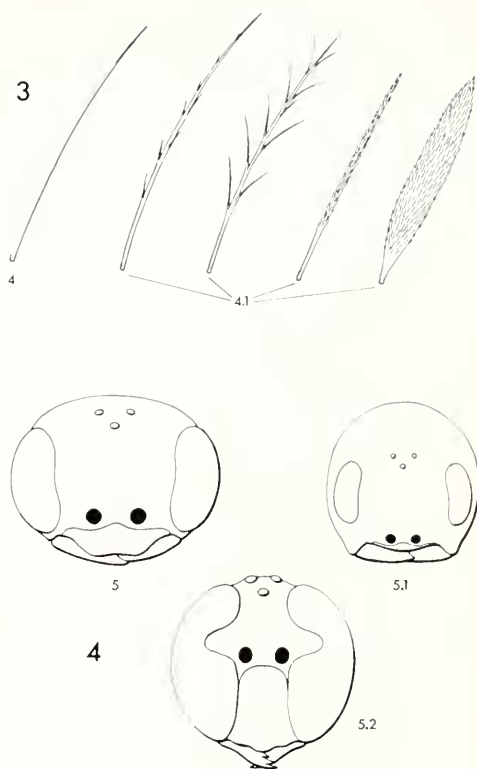
The development of a sterile worker caste (3.1) is characteristic of the entire formicid group only, and thus provides no information on relationships at the higher levels. However, a similar derived state has evolved independently on various occasions within the apid (e.g., *Lasioglossum*, *Bombus*, *Apis*, *Trigona*; Michener, 1974) and vespid (e.g., *Vespa*, *Vespula*; Wilson, 1971) groups.

4. *Pubescence* (Fig. 3). Primitively, all pubescence is simple and unbranched. 4.1—Some of the body setae, especially those dorsally at the base of the metasoma, are branched to some extent, being sub-plumose or plumose.

Simple pubescence is considered primitive because this is the condition in most Hymenoptera, both non-aculeates and aculeates.

The presence of plumose pubescence is characteristic of the apid group and is one of the classical characters for distinguishing this group from the sphecids. State 4.1 also occurs on internode 21-22, however, associating the cotillid and typhoctid groups. A similar state has developed within the anthoboscid (e.g., *Lalapa*) and mutillid (e.g., *Sphaerophthalma*, *Pseudomethoca*) groups at least, so that the importance of this character and its usefulness for establishing higher groupings is somewhat diminished.

5. *Clypeus* (Fig. 4). Primitively, the clypeus is rather short and transverse so that



FIGS. 3-4. Characters of Aculeata. 3, body seta, showing primitive and derived states of pubescence; 4, head, anterior view, showing primitive and derived states of clypeus (5 based on *Anthobosca*, ♂; 5.1 on *Clystopenella*, ♀; 5.2 on *Apoica*, ♂).

the antennae are inserted below the middle of the face but not immediately above the oral cavity, i.e., the clypeus is termed "moderate." 5.1—The clypeus is extremely short and reduced to a transverse strip so that the antennae appear to be inserted just above the oral cavity. 5.2—The clypeus is somewhat dorsally produced and increased in height so that the antennae are inserted at or slightly above the middle of the face.

A moderate clypeus is considered primitive because this is the condition in most Aculeata and in particular in those considered primitive on the basis of other, stronger characters. Most non-Aculeata appear to have a slightly larger clypeus, although the Trigonalidae seem to fall

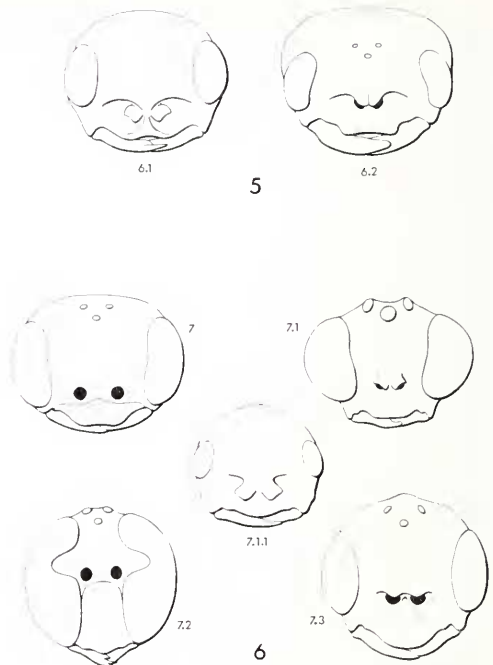
more or less midway between clear expression of either the primitive state or state 5.2.

The clypeal form is difficult to interpret and is somewhat variable so that the states are fairly equivocal. However, state 5.1 represents an extreme and is characteristic of the scolebythid group as well as the females of the brachycistidid group. It also occurs within at least the myzinid group (e.g., female of *Braunsomeria*) and there is a tendency toward this state in the females of the bradynobaenid group. State 5.2 (representing the opposite trend) is present in the scoliid group (although somewhat equivocally so) and more clearly in the vespids (thus arising on internode 19-20), and in the males of the apterogynid group. It has also arisen within various other taxa such as the apid (practically all members except e.g., *Brachyhesma*), sphecid (e.g., *Sphex*, *Zyzzyx*) and formicid (especially males, e.g., *Paltothyreus*, *Campopotus*) groups. In view of the sporadic occurrence of both derived states and their equivocal nature, the clypeal form is accorded little weight in the analysis of relationships.

\*6. *Antennal socket* (Fig. 5). Primitively, the antennal socket is an approximately circular foramen bordered evenly by a slightly raised rim. 6.1—The dorsomesal region of the rim is much produced, forming a projecting "tubercle" which is semi-circular in cross-section and well-differentiated from the interantennal frontal region. 6.2—The interantennal front dorsomesal to the antennal socket is produced into a "frontal ledge" which is not highly differentiated from the front dorsally and is thus distinguishable from state 6.1.

A simple antennal socket is considered primitive because this is the condition in most non-aculeate Hymenoptera as well as most Aculeata.

State 6.1 occurs twice on the cladogram, on internodes 7-8 (where it associates the



Figs. 5-6. Characters of Aculeata. 5, head, anterior view, showing derived states of antennal socket (6.1 based on *Aureotilla*, ♀; 6.2 on *Meria*, ♀); 6, head, anterior view, showing primitive and derived states of eye form (7 based on *Anthobosca*, ♂; 7.1 on *Apterogyna*, ♂; 7.1.1 on *Apterogyna*, ♀; 7.2 on *Apoica*, ♂; 7.3 on *Methocha*, ♂).

sapygid, myrmosid and mutillid groups) and 21-23 (linking the chyphotid and apterogynid groups), being subsequently modified into state 6.2 in the bradynobaenid group. State 6.2 occurs elsewhere on internode 12-13 thus linking the myzinid and methochid groups although it is not as well-developed in many of the methochids as in most myzinids. Although there is a tendency toward a state like 6.2 in female *Plumarius*, this state is not considered to be fully developed in the plumariid group. States 6.1 and 6.2 are not as distinct as the notation would indicate, as witness the apparent derivation of 6.2 directly from 6.1 in the bradynobaenid group. A state similar to 6.1 also occurs within the bethylid group (e.g., *Apenesia*, *Pristocera*), so that this character is ac-

tually not an extremely efficient indicator of groupings.

7. *Eye form* (Fig. 6). Primitively, each compound eye is large, oval and with the inner margin (seen from directly anteriorly) shallowly sinuate. 7.1—The eye is somewhat rounded but retains the sinuate inner margin. 7.1.1—The eye is rounded and the inner margin is convex. 7.2—The eye is essentially oval but the inner margin is deeply incised so that the shape is reniform. 7.3—The eye is oval but the inner margin is convex.

An oval eye with sinuate inner margin is considered primitive because this is the condition in most non-Aculeata and also in those aculeates considered to be the most primitive on the basis of other characters.

The differences between the various states of eye form are very subtle and often equivocal. Nevertheless, they do seem to provide useful information on higher groupings. Although state 7.1 has apparently evolved in parallel in both the chypotid and apterogynid groups and its derivative occurs in the females of both these groups, there is a trend toward this state in the bradynobaenid group also, so that state 7.1 may logically be placed on internode 21-23 as another synapomorphy shared by these three taxa. A limitation is, however, inherent in the usefulness of this state since similar states have occurred within the plumariid (e.g., *Plumarius* male—7.1), brachycistidid (e.g., *Brachycistis*—7.1), mutillid (e.g., *Chrestomutilla*—7.1; *Sphaerophthalma*—7.1.1), formicid (most females—7.1.1) and other groups. State 7.2 is uniquely derived on the tree and links the scoliid and vespid groups, falling on internode 19-20. The strength of this is somewhat lessened by the occurrence of a similar condition within the sphecid (e.g., *Trypargilum*), anthoboscid (e.g., *Lalapa*), sapygid (e.g., *Sapyga*), mutillid

(*Rhopalomutilla*, *Mutilla* males), myzinid (e.g., *Myzinum* male) and rhopalosomatid (e.g., *Rhopalosoma*) groups also. State 7.3 has occurred on at least four separate occasions, in the plumariid (female), scolebythid, methochid and brachycistidid (female) groups. It also has arisen within various taxa such as the bethylid (e.g., *Parnopes*), sphecid (e.g., *Cerceris*) and rhopalosomatid (e.g., *Olixon*) groups so that it is of little significance in delineating relationships.

8. *Eye contour*. Primitively, the compound eye more or less follows the general contours of the head. 8.1—The eye is protuberant and very prominent, being highly differentiated from the surrounding cuticle.

A non-protuberant eye is considered primitive because this is the condition in most non-aculeates and also in most aculeate Hymenoptera.

Although state 8.1 has apparently occurred as a parallelism in both the chypotid and apterogynid groups, it may actually be that there has been a reversal in the bradynobaenid group to a situation similar to the primitive state, a hypothesis possibly supported by the fact that the eyes do not merge smoothly into the surrounding cuticle but present a discontinuity at their margins in the males of the bradynobaenids. In this case state 8.1 would have arisen on internode 21-23. In the absence of any further indications, parallel derivations are considered more likely than is the reversal. Elsewhere, state 8.1 occurs in the brachycistidid group and also within the plumariid (e.g., *Plumarius* male), mutillid (e.g., *Sphaerophthalma*) and formicid (e.g., *Paraponera* male) groups, especially in those species of nocturnal or crepuscular habit. This character is probably thus of minimal significance in establishing relationships between the taxa investigated.

9. *Eye pores and setae.* Primitively, the compound eye has scattered pores which penetrate the cuticle between the ommatidia and which bear minute setae which are not readily distinguishable except under extreme magnification (referred to as "not evident"). 9.1—The setae are readily visible at magnifications of approximately 100 $\times$ , and are referred to as "short." 9.2—The sensory setae are obvious at magnifications of 20 $\times$  or less and are referred to as "moderately long." 9.3—The pores and setae are apparently completely absent and are not visible under magnifications of 100 $\times$ .

An eye with pores and minute setae is considered primitive because this is the condition in most non-aculeates (in particular the Terebrantia, including Trigonalidae) and also in most Aculeata.

It is often extremely difficult to distinguish the various states involved in this character and each has apparently arisen independently on several occasions, so that they are of minimal significance in the delineation of the cladogram. State 9.1 is characteristic of the scolebythid, brachycistidid (male), sierolomorphid, rhopalosomatid and formicid groups and also links the eotillid, typhoctid and males of the chyphotid groups (on internode 18-21). It has apparently been modified in the females of the chyphotids and both sexes of the apterogynid and bradynobaenid groups, the last three groups being associated by possession of state 9.3 (on internodes 21-23 for the female and 23-24 for the male). State 9.1 has also evolved independently within the bethylids (e.g., *Pristocera*). State 9.2 appears in the myrmosids and methochids and also within the apids (e.g., *Apis*, *Coelioxys*) and mutillids (e.g., *Arcotilla*). Apart from its occurrences in the branch subtended by internode 21-23, state 9.3 appears in the plumariid (female), brachycistidid (female) and scoliid groups and also within

the plumariid (e.g., *Plumarius* male) and mutillid (e.g., *Pseudophotopsis*) groups at least.

10. *Ocelli.* Primitively, three ocelli are present on the vertex. 10.1—The ocelli are completely absent, not even traces being retained.

The presence of ocelli is considered primitive because this is the condition in most Hymenoptera (both Aculeata and non-aculeates) and also in most insects.

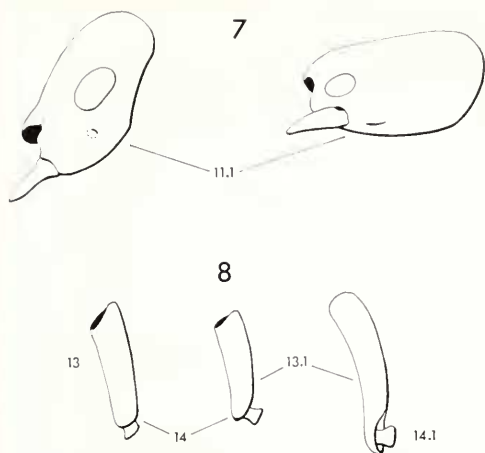
The complete loss of ocelli is almost invariably associated with aptery although the inverse relationship does not always hold. Thus state 10.1 has appeared in the females of the plumariid and brachycistidid groups and also in the females of the entire branch subtended by internode 18-21. It is also present within the bethylid (e.g., *Pristocera* female; Evans, 1964a), mutillid (all females except some *Pseudophotopsis*), myrmosid (e.g., *Myrmosula* female), rhopalosomatid (e.g., *Olixon*) and formicid (most workers) groups. In addition, some or all of the ocelli are greatly modified or reduced (although traces generally remain) in various members of the sphecid group (e.g., some *Bembix*; Evans, 1966a). State 10.1 is thus of little or no cladistic significance.

\*11. *Genal organ* (Fig. 7). Primitively, the gena is simple, without any specialized organ. 11.1—The gena bears an apparently secretory organ opening externally via an invaginated line or scattered pores.

A simple gena is considered primitive because this is the condition in most non-Aculeata (if not all of them) and also in most aculeates.

The development of a genal secretory organ in the apterogynid and bradynobaenid groups is apparently unique in the Aculeata and thus provides a very good synapomorphic character associating these two groups (on internode 23-24). The organ has a slightly different appearance in the two groups, forming a slight pro-





FIGS. 7-8. Characters of Aculeata. 7, head, lateral view, showing derived state of genal organ (11.1 based on *Apterogyna*, ♀, and *Bradynobaenus*, ♀, left to right); 8, antennal scape, anteromesal view, showing primitive and derived states of radicle axis and radicle-scape insertion (13, 14 based on *Zyzyx*, ♀; 13.1, 14 on *Chyphotes*, ♂; 13.1, 14.1 on *Aureotilla*, ♂).

tubercle in the female of apterogynids and not being raised in the female bradynobaenids. Nevertheless it seems clear that the two forms are homologous. In male apterogynids it forms a patch of scattered pores and is not clearly distinguishable in bradynobaenid males. The organ may be analogous to the "felt line" on the second metasomal tergum (character 70).

\*12. *Antennal dimorphism*. Primitives, the antenna comprises the same number of segments (usually 13) in both sexes. 12.1—The number of antennal segments is 12 in the female and 13 in the male.

A condition with the antenna 13-segmented in the male and 12-segmented in the female is unique in the Hymenoptera to most groups of Aculeata, those aculeates in which it does not occur being considered primitive on the basis of other characters also. This particular sexual dimorphism is thus considered derived.

Almost all groups of Aculeata show state 12.1 with great consistency, this apparently being a condition which evolved early and which serves to link almost all

the aculeates into a holophyletic group (on internode 1-4). Only the plumariid, bethylid and scolebythid groups typically show no sexual dimorphism in the number of antennal segments. Within the bethylid group there is much variation in the number of segments (from 10 to 40; Riek, 1970) but the number is usually the same in both sexes or fewer in the males. The importance of state 12.1 is not much diminished by the fact that it has apparently been reversed on rare occasions within some taxa, such as in the pompilid group (e.g., *Cteniziphontes*; Evans, 1972) and the mutillid group (*Atillum*, *Hoplocrates*) where both sexes have the antenna 13-segmented. In addition, the number of segments has been reduced to 12 in both sexes in a few instances, for example within the vespids (e.g., *Belonogaster*) and apids (e.g., *Neopasites*; Linsley & Michener, 1939), and some dacetine ants have as few as four antennal segments in the female (Brown & Taylor, 1970).

13. *Radicle axis* (Fig. 8). Primitives, the axis of the radicle does not deviate much from that of the remainder of the scape, so that the scape merely has a somewhat differentiated annulus basally. 13.1—The axis of the radicle forms a marked angle with that of the remainder of the scape.

A scape with a simple radicle is considered primitive because this is the condition in most non-aculeates as well as most Aculeata.

An angulate radicle (13.1) appears three times on the cladogram, in the plumariids (female) and on internodes 8-9 (linking the myrmosids and mutillids) and 21-23 (associating the chyphotid, apterogynid and bradynobaenid groups). Nevertheless, similar states are present within various other taxa such as the bethylids (e.g., *Bethylus*, *Anisepyris*), myzinids (e.g., *Meria*) and thynnids (e.g., *Elaphroptera*) so that this state is actually not very useful in delineating relationships.

\*14. *Radicle-scape insertion* (Fig. 8). Primitively, the radicle is demarcated by a simple annular constriction. 14.1—The scape is produced externally into a flange that forms a cup-shaped depression or invagination into which the radicle is set.

A simple radicle-scape insertion is considered primitive because this is the condition in most Hymenoptera, both non-aculeates and aculeates.

The invagination of the radicle appears once on the tree, on internode 8-9, thus associating the myrmosid and mutillid groups strongly. Although a similar development has occurred within the bethylid group (e.g., *Aniseopyris*), such species are almost certainly only remotely related to the myrmosid-mutillid group, so that this affects the usefulness of this character minimally.

15. *Labio-maxillary complex* (Fig. 9). Primitively, the labio-maxillary complex is well-developed but relatively short and adapted for lapping. 15.1—The labio-maxillary complex is elongated by production of the prementum and stipes only. 15.2—The labio-maxillary complex is elongated by production of the glossa and paraglossa only. 15.3—The labio-maxillary complex is elongated by production of the glossa and paraglossa only. 15.4—The labio-maxillary complex is much reduced in size.

A well-developed but relatively short labio-maxillary complex is considered primitive because this is the condition in most non-Aculeata and also in most aculeates.

Derived states 15.1, 15.3 and 15.4 are each present in only one taxon, the apid, sapygid and bradynobaenid groups respectively, thus not contributing any information on higher groupings. State 15.2 is apparently possessed in common by the scoliid and vespid groups, seemingly having arisen on internode 19-20. There is some uncertainty about this, however, since the labio-maxillary complex is somewhat different in form in the two taxa, although its slight elongation in both has involved the same structures. In addition, many bees have a modification similar to state 15.2 superimposed on state 15.1.

16. *Maxillary palpus*. Primitively, the maxillary palpus is six-segmented. 16.1—The maxillary palpus is five-segmented. 16.2—The maxillary palpus is two-segmented.

A six-segmented maxillary palpus is considered primitive because this is the condition in most aculeates and many non-aculeates, this being the maximal number of segments in the Hymenoptera. This is also probably the primitive condition for the Insecta (Matsuda, 1965).

A five-segmented palpus (16.1) is characteristic of the female of the plumariid group. Nevertheless, similar reductions in

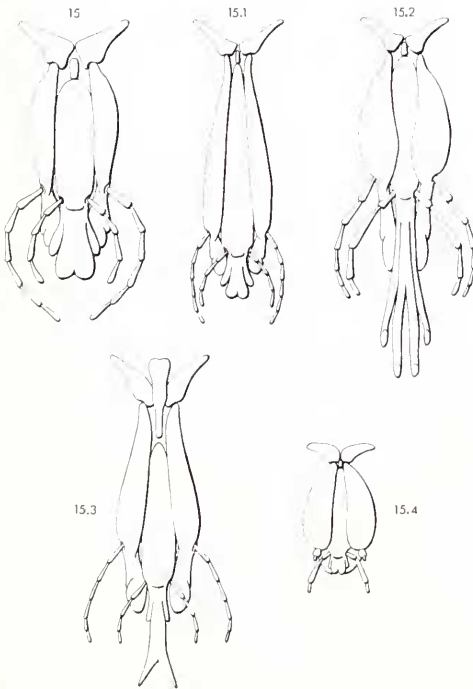


FIG. 9. Labio-maxillary complex, ventral view, somewhat diagrammatic, showing primitive and derived states (15 based on *Anthobosca*, ♂; 15.1 on *Callomelitta*, ♀; 15.2 on *Monobia*, ♀, modified; 15.3 on *Fedtschenkiä*, ♀; 15.4 on *Bradynobaenus*, ♀, cardines may differ from form shown).

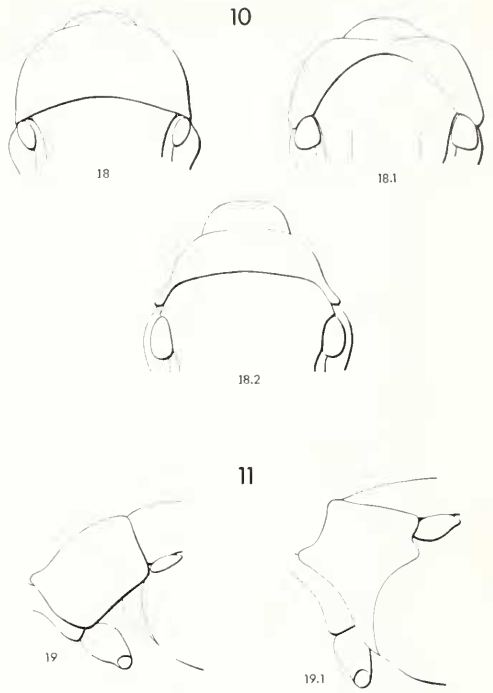
the number of segments have occurred within many of the other taxa, such as the bethylid group (e.g., *Dissomphalus* male; Evans, 1964a), the male of *Plumarioides* in the plumariid group, and the apid group (where the number of segments ranges from 6 to 0). This state is thus not of great significance, especially since it involves the loss of only one segment. State 16.2 involves the loss of four segments and has occurred in the bradynobaenid group and elsewhere such as within the bethylid (e.g., *Dissomphalus* female; Evans, 1964a), mutillid (*Rhopalomutilla* female) and apid (e.g., *Apis*) groups. It is thus of no use in establishing higher groupings.

17. *Labial palpus*. Primitively, the labial palpus is four-segmented. 17.1—The labial palpus is three-segmented.

A four-segmented labial palpus is considered primitive because this is the condition in many non-Aculeata and in most aculeates; it also represents the maximal number of segments in the Hymenoptera. The primitive condition for the Insecta is, however, probably three segments (Matsuda, 1965).

The loss of one segment in the labial palpus has apparently occurred on the tree at least three times independently, in the plumariid (female), bethylid and bradynobaenid groups. It is also found within the plumariid group (e.g., males of *Myrmecopterina*, *Plumarius*). It is thus of no use in delimiting higher groupings.

\*18. *Hind margin of pronotum* (Fig. 10). Primitively, the pronotum is large and somewhat saddle-shaped with its hind margin nearly straight and only very slightly anteriorly arcuate. 18.1—The pronotum is shortened with its hind margin strongly concave in a fairly regular and somewhat acute parabolic curve (roughly V-shaped). 18.2—The pronotum is shortened with its hind margin shifted anteri-



FIGS. 10-11. Characters of Aculeata. 10, anterior region of mesosoma, dorsal view, showing primitive and derived states of hind margin of pronotum (18 based on *Anthobosca*, ♀; 18.1 on *Trielis*, ♀; 18.2 on *Cerceris*, ♀); 11, anterior region of mesosoma, lateral view, showing primitive and derived states of pronotal articulation (19 based on *Anthobosca*, ♀; 19.1 on *Scolia*, ♀).

only over almost its entire width (broadly U-shaped).

A large pronotum with approximately straight hind margin is considered primitive because this is the condition in those groups of Aculeata considered primitive on the basis of other characters, and also in various of the most primitive non-aculeates (e.g., xyelids). Furthermore, elsewhere in the insects reduction in relative size of the pronotum is generally derived.

State 18.1 has arisen independently on at least six occasions, on internodes 18-19 and 21-23 (males), and in the plumariids (male), mutillids, brachycistidids (male) and rhopalosomatids. It is thus of little use in establishing relationships. By con-

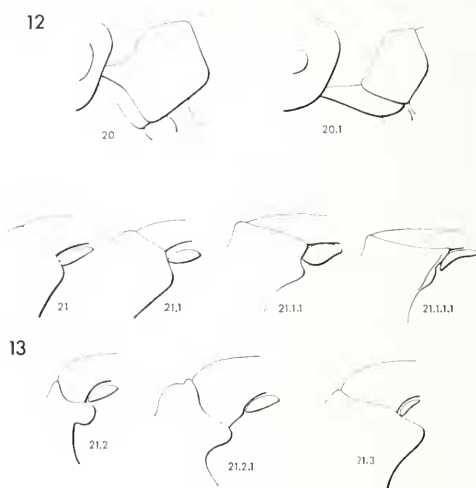
trast, state 18.2 has apparently arisen only once, on internode 4-5, thus associating the sphecids and apid groups. A vaguely similar condition is present in some members of the bethylid group (e.g., *Deinodryinus*, *Euchroeus*) causing some authors to consider *Ampulex* (definitely a sphecid although it has the pronotum larger than most other sphecids; see Evans, 1959a; Leclercq, 1954) closer to (or even a member of) the bethylid group (e.g., Nagy, 1969a). The condition in the Trigonalidae is also vaguely similar to state 18.2. However, in all three of these instances there are marked differences in detail (especially in the form of the posterolateral angle and the spiracular lobe) so that these superficially similar states appear definitely to have had independent origins.

\*19. *Pronotal articulation* (Fig. 11). Primitively, the attachment of the pronotum to the mesothorax is loose and freely articulating. 19.1—The pronotum is very closely attached and coadapted to the mesothorax so that no or extremely little movement is possible between them, although the sclerites are not actually fused.

A freely movable connection between the pronotum and mesothorax is considered primitive because this is the condition in most non-aculeates as well as in most Aculeata.

Apparently immovable association of the pronotum and mesothorax has occurred in only two taxa, the scoliid and vespidae groups, and is so similar in both that it is considered as very good evidence for their association, this state thus having arisen on internode 19-20.

20. *Pronotal collar* (Fig. 12). Primitively, the pronotum is expanded anteriorly as a well-developed flange or "collar" which aids in the support of the head and provides protection to the neck region dorsally. 20.1—The pronotum is somewhat flattened anteriorly and not at all ex-



FIGS. 12-13. Characters of Aculeata. 12, prothorax and base of head, lateral view, showing primitive and derived states of pronotal collar (20 composite; 20.1 based on *Clystospennella*); 13, anterodorsal region of mesosoma, lateral view, showing primitive and derived states of posterolateral angle of pronotum (21 based on *Anthobosca*, ♂; 21.1 on *Pseudophotopsis*, ♂; 21.1.1 on *Scolia*, ♀; 21.1.1.1 on *Rygchium*, ♀; 21.2 on *Callomelitta*, ♀; 21.2.1 on *Trypargilum*, ♀; 21.3 on *Bradynobaenus*, ♂).

panded, so that the neck region is dorsally exposed.

A well-developed pronotal "collar" is considered primitive because this is the condition in most non-Aculeata (although generally not well-developed in Symphyta) as well as in practically all aculeates.

Although the derived state is approached in various taxa (e.g., the vespidae), it is fully expressed only in the plumariid (female) and scolebythid groups, and in a different fashion in each. State 20.1 is thus of no use in establishing relationships between taxa.

\*21. *Posterolateral angle of pronotum* (Fig. 13). Primitively, the posterolateral angle of the pronotum is evenly rounded, reaching the tegula but not exceeding its anterior margin. 21.1—The posterolateral angle is very slightly dorsally produced so as to appear truncate anterior to the

tegula; it attains the tegula but does not exceed its anterior margin. 21.1.1—The posterolateral angle is dorsally produced and exceeds the anterior margin of the tegula very slightly so that the lobe is notched. 21.1.1.1—The posterolateral angle is markedly produced dorsally and posteriorly so that it exceeds the level of the tegula and forms an acute lobe above it. 21.2—The posterolateral angle is reduced dorsally above and slightly anterior to the spiracular operculum; the operculum forms a highly differentiated lobe reaching the tegula. 21.2.1—The posterolateral angle is reduced anterodorsal to the spiracular operculum and is somewhat retracted anteriorly so that the highly differentiated operculum does not reach the level of the tegula. 21.3—The posterolateral angle is slightly posteriorly produced below the tegula and thus exceeds its anterior margin slightly, forming a fairly acute lobe.

A simple posterolateral angle which reaches the tegula is considered primitive because this is the condition in many non-aculeates (especially Symphyta; many Terebrantia show differing modifications) and also in many Aculeata, in those taxa which are generally considered most primitive on the basis of other characters.

A slight dorsal production of the pronotal angle (22.1) has apparently occurred on at least four occasions, on internodes 12-14 and 18-19 and in the mutillid and rhopalosomatid groups, and is thus not of much use in establishing relationships. However, further development of this structure has occurred in both taxa derived from internode 19-20; state 21.1.1 arose on internode 19-20, being present in the scoliid group, and its further elaboration (21.1.1.1) is present in the vespidae group. This derivation of state 21.1.1 is unique and thus provides good evidence of the close relationship of the scoliid and vespidae groups. State 21.2 arose uniquely on inter-

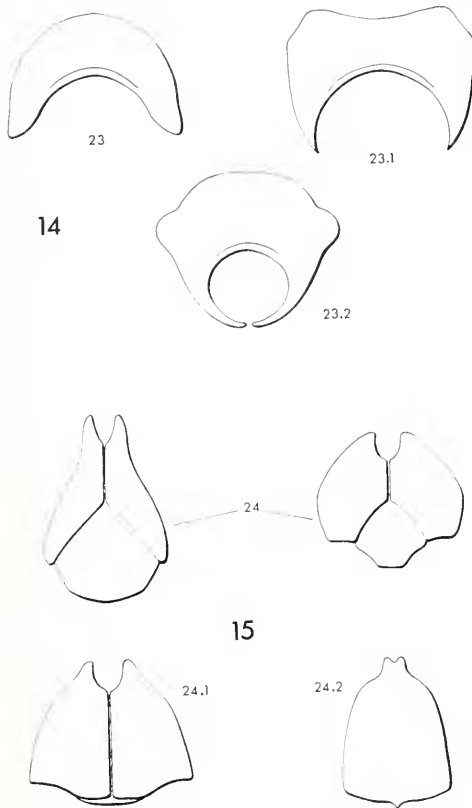
node 4-5 and thus is a very good indicator of the holophyly of the sphecidae and apidae groups. Its elaboration (21.2.1) has occurred in the entire sphecidae group, although it is not very well-developed in some (such as *Astata*) and a similar state is present in most of the apids (but 21.2 in *Callomelitta* and *Megachile*, e.g.). A superficially similar condition is also present within the bethylid group (e.g., *Chrysis*, *Euchroeus*) but this anterior retraction of the spiracular operculum differs in detail from the state in the sphecids, so that it does not diminish the significance of state 21.2.1 or its antecedent. State 21.3 is apparently unique to the bradyobaenid group although a slight tendency toward this state is distinguishable in the apterogynids, so that its importance in delimiting higher groupings is minimal.

22. *Posteroventral margin of pronotum*. Primitively, the posteroventral margin of the pronotum is approximately straight. 22.1—The posteroventral margin is distinctly concave.

An approximately straight posteroventral margin is considered primitive because this is the condition in many non-aculeates (in particular Symphyta) and also in many of the Aculeata which are considered to be the most primitive on the basis of other characters.

The derived state represents a widespread tendency that has arisen on at least four occasions and has been reversed at least once. Thus, state 22.1 appears on internodes 4-5, 12-14 and 6-15, and in the methochid group. The apparently primitive state has been regained on internode 21-22. Because of its plasticity and the somewhat equivocal nature of this character, it is not of much utility in demonstrating relationships, although it does seem to have some value in indicating which taxa are relatively more advanced than others.

\*23. *Ventral angle of pronotum* (Fig. 14).



FIGS. 14-15. Characters of Aculeata. 14, pronotum, anterior view, showing primitive and derived states of its ventral angle (23 based on *Anthobosca*, ♀; 23.1 on *Synoecca*, ♀; 23.2 on *Cerceris*, ♀); 15, prothorax, ventral view, showing primitive and derived states of propleural separation (24 based on *Clystopenella*, ♀, and *Enchroeus*, ♂, left to right; 24.1 on *Enclavelia*, ♀; 24.2 on *Plumarius*, ♀).

Primitively, the ventral angle of the pronotum is rounded and does not much (or at all) exceed the level of the base of the forecoxa ventrally. 23.1—The ventral angle is acute and produced ventrally beyond the forecoxal base. 23.2—The ventral angle is greatly produced so that it almost contacts its counterpart midventrally.

A rounded ventral angle is considered primitive because this is the condition in most non-aculeates as well as in most Aculeata.

State 23.1 has apparently arisen twice on the cladogram, on internodes 18-19 (as-

sociating the formicid, vespid and scoliid groups) and 21-23 (associating the chypnotid, apterogynid and bradynobaenid groups). Although it is also weakly present within the plumariid group (e.g., male of *Plumarius*), it seems to be fairly useful and may actually represent a trend originating on internode 16-18. The extreme development of the ventral angle (23.2) is uniquely present in the sphecid and apid groups and apparently arose on internode 4-5, thus forming a strong indicator of the holophyly of this grouping.

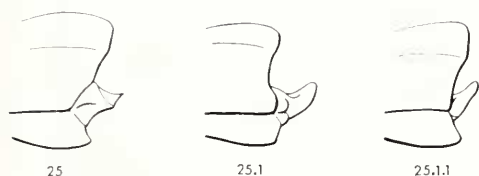
\*24. *Propleural separation* (Fig. 15). Primitively, the propleura are separated posteriorly, diverging at an angle and thus exposing the prosternum anterior to the forecoxae. 24.1—The propleura are mesally contiguous posteriorly and do not diverge at an angle; their posterior margins form a more or less straight line, so that the prosternum is not visible between the propleura. 24.2—The propleura are modified similarly as in 24.1 but they are fused along the midline both dorsally and ventrally.

Posteriorly diverging propleura are considered primitive because this is the condition in many non-Aculeata (except that various taxa highly specialized in other respects, as well as the Trigonalidae, show a tendency toward a state approaching 24.1) and in those aculeates which possess many other characters in their primitive states.

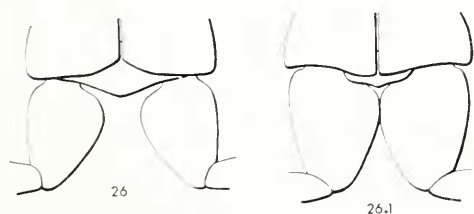
The primitive extreme is apparently present in the scolebythid group where the prosternum is remarkably well-developed anteriorly and is extensively exposed between the widely diverging propleura. Since this condition is more extreme than in any other taxon, it may be a secondary development, however. State 24.1 is uniquely developed in all the taxa subtended by internode 4-6, although the superficially similar 24.2 is present in the

female plumariids where the propleura form a rigid tube. This character is probably not as reliable as might be supposed, however, since some members of the sphecid (e.g., *Crabro*) and apid (e.g., *Sericogaster*) groups show conditions approaching state 24.1.

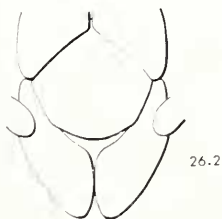
\*25. *Prosternum* (Fig. 16). Primitively, the prosternum forms an approximately uniform plane and is not sunken except perhaps for a very short posterior section. 25.1—The prosternum is sunken over most of its surface so that only a short anterior section (shorter than the sunken section) is visible ventrally, this section being in a different plane from the remainder of the



16



17



FIGS. 16-17. Characters of Aculeata. 16, posterior region of propleura and prosternum, oblique ventrolateral view, showing primitive and derived states of prosternum (25 based on cleptid sp.: 25.1 on *Anthobosca*, ♀; 25.1.1 on *Polybia*, ♀); 17, posterior region of prothorax, ventral view, showing primitive and derived states of forecoxal contiguity (26 based on cleptid sp.: 26.1 on *Anthobosca*, ♂; 26.2 on *Clystospenella*, ♀).

sternum. 25.1.1—The prosternum is entirely sunken and not visible ventrally.

A prosternum with most of its surface in a single plane is considered primitive because this is the condition in most non-aculeates. (Even though the prosternum may be somewhat hidden in many, e.g., the Trigonalidae, even in these it generally forms a single plane.)

State 25.1 has apparently arisen on at least two occasions in the aculeates, in the plumariid group and on internode 1-4. It is additionally present within the bethylid group (e.g., *Pristocera*). The second derived state (25.1.1) apparently has a unique origin (on internode 19-20) and associates the vespidae and scoliid groups. Since the difference between 25.1 and 25.1.1 is not very great, however, this state may not be as valuable as its apparent unique derivation would indicate.

\*26. *Forecoxal contiguity* (Fig. 17). Primitively, the forecoxae are somewhat separated basally by the width of the relatively well-developed prosternum. 26.1—The forecoxae are contiguous basally due to reduction in the posterior width of the sternal region. 26.2—The forecoxae are basally separated but are posteriorly produced beyond the trochanteral insertions so as to become contiguous apically only.

Separated forecoxae are considered primitive because this is the condition in most non-Aculeata, although there is much variation and the forecoxae approach contiguity in various groups (including the Trigonalidae).

Although there is variation in the intercoxal distance in the bethylid and plumariid groups so that some members have the forecoxae almost contiguous, actual contiguity (26.1) apparently arose uniquely on internode 1-4. State 26.2 is uniquely derived and occurs only in the scolybythid group, thus not contributing information on relationships.

27. *Mesonotum*. Primitively, the mesonotum does not extend anteriorly much beyond the level of the tegulae. 27.1—The mesonotum is mesally anteriorly produced so that its anterior margin extends much anterior to the level of the tegulae.

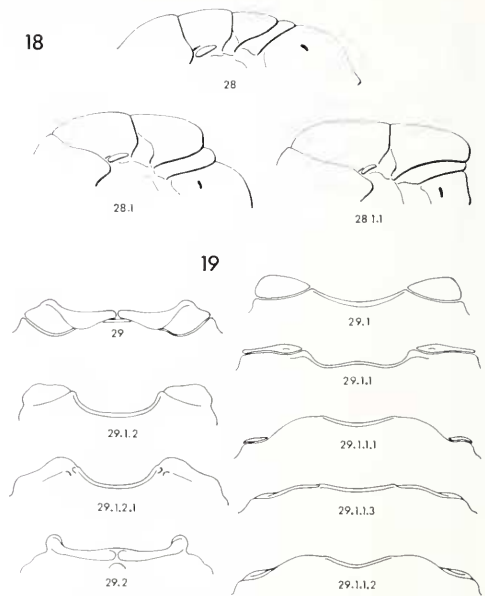
A short mesonotum is considered primitive because this is the condition in those Aculeata considered to be generally the most primitive on the basis of other characters, and is also the condition in the most primitive non-aculeates (e.g., Xyelidae).

State 27.1 has arisen on at least six separate occasions, on internodes 18-19 and 21-23 (males), in the plumariid (male), brachycistidid (male) and rhopalosomatid groups, and somewhat less obviously on internode 4-5. It is thus essentially useless for associating groups. This state is logically linked with the derived states of character 18, but does not present an identical distribution on the cladogram and is thus not considered a duplication.

\*28. *Scutellum* (Fig. 18). Primitively, the mesoscutellum is simple, more or less flattened and not highly differentiated from the remaining notal area. 28.1—The scutellum is enlarged, being posterodorsally swollen and evenly protuberant. 28.1.1—The scutellum is extremely enlarged and produced so that it overhangs the mesonotum.

A simple scutellum is considered primitive because this is the condition in most non-aculeates as well as in most members of the Aculeata.

Although there are scattered instances of enlargement of the scutellum (e.g., apids, *Euglossa*; mutillids, *Trispilotilla*; formicids, *Atta*) these are of varying types, and a swollen scutellum is characteristic of only two of the taxa considered, the apterogynid and bradynobaenid groups. State 28.1 has thus apparently arisen on internode 23-24 and is considered to be quite good evidence of the grouping of



FIGS. 18-19. Characters of Aculeata. 18, dorsal region of mesosoma, lateral view, showing primitive and derived states of scutellum (28 based on *Anthobosca*, ♀; 28.1 on *Apterogyna*, ♂; 28.1.1 on *Bradynobaenus*, ♂); 19, anterior region of mesopleurosternum, ventral and lateral view (as if flattened), showing primitive and derived states of prepectus (29 based on *Cleptes*, ♀; 29.1 on *Sierolomorpha*, ♀; 29.1.1 on *Chyphotes*, ♂; 29.1.1.1 on *Polistes*, ♀; 29.1.1.2 on *Trielis*, ♂; 29.1.1.3 on *Paraponera*, ♂; 29.1.2 on *Fedtschenkia*, ♀; 29.1.2.1 on *Pseudophotopsis*, ♂; 29.2 on *Chlorion*, ♀).

these two taxa although it has been taken a step further in the bradynobaenids where state 28.1.1 is present.

\*29. *Prepectus* (Fig. 19). Primitively, the prepectus (= epinemium) is a transverse sclerite divided midventrally but with the halves contiguous (or almost so), extending across the anterior margin of the mesopleurosternum and articulating freely with this margin. 29.1—Each half of the prepectus is narrowed so that the two sections become widely separated and do not extend to the ventral surface of the mesosoma but do extend the entire height of the pleural region laterally. 29.1.1—Each section of the prepectus is widely separated from its counterpart and is shortened so that each half forms a very short but



elongate strip at the anterior margin of the mesepisternum; the articulation is retained and the prepectal sclerite is hidden under the posteroventral margin of the pronotum. 29.1.1.1—Each prepectal sclerite is very narrow and short, extending over only the dorsal half or less of the mesepisternum and articulating with it; the sclerite is hidden under the posterolateral angle of the pronotum. 29.1.1.2—Each prepectal sclerite is extremely short and narrow, extending over less than the dorsal half of the mesepisternum and fused to it with almost no trace of differentiation; the sclerite is hidden under the posterolateral angle of the pronotum. 29.1.1.3—Each prepectal sclerite is shortened but extends over most of the height of the mesepisternum and is fused to it; the sclerite is hidden under the posteroventral margin of the pronotum. 29.1.2—Each prepectal sclerite is not shortened and extends the height of the mesepisternum, being fused to it with the line of fusion forming a sulcus. 29.1.2.1—Each prepectal sclerite is not shortened and extends the height of the mesepisternum, being fused to it but with the line of fusion obliterated except for a pair of pits ventrally. 29.2—The prepectus extends completely across the anterior margin of the mesopleurosternum, is fused in the midline and is also fused to the pleurosternum, forming a depressed anterior margin to it.

The allocation of states of the prepectus is that which shows greatest correlation with the groupings made on the basis of other characters. A state similar to 29.2 is present in Trigonalidae and some chalcidoids, however. Although the sequence and pattern of modification forms a logical scheme, the homologies of the sclerites involved are somewhat uncertain despite the studies by Snodgrass (1910, 1935), Matsuda (1970) and others. In particular, the possibility of confusion of the “postspirac-

ular sclerite” (probably the anepisternum) and the “epicnemium” (prepectus) has been noted by Richards (1956a; see also 1956b, 1971). Additional investigations, especially of groups not critically studied hitherto, should clarify the situation.

The primitive state is present in the bethylid, scolebythid and plumariid groups, although some members of the last (e.g., *Plumaroides*) have the prepectus tending towards state 29.1. Apart from this, state 29.1 has apparently been derived only on internode 4-6, thus associating the remainder of the aculeates except for the sphecids and apids. State 29.1.1 has apparently arisen on three occasions, on internode 16-18 (where it groups eight taxa) and in the brachycistidid and rhopalosomatid groups. The next modification (29.1.1.1) has occurred only in the vespid group. Even greater fusion and reduction (29.1.1.2) has occurred in the scoliid group and state 29.1.1.3 is characteristic only of the formicid group. Modification in a different direction (29.1.2) has apparently occurred twice, on internode 7-8 (associating the sapygid, myrmosid and mutillid groups) and in the pompilid group. The next step in this sequence (29.1.2.1) has occurred once, on internode 8-9, linking the myrmosid and mutillid groups even more strongly. State 29.2 is characteristic of the sphecid and apid groups and serves to emphasize their relatively basal position, this state occurring on internode 4-5. A few members of the bethylid group (e.g., *Pseudisobrachium coxalis*) show a similar condition, however, this fact somewhat reducing the strength of this state in associating the sphecids and apids. Although a more detailed investigation of these structures is necessary, the pattern of evolution derived here seems to provide useful phyletic information. Although Reid (1941) misinterpreted the situation in some taxa (e.g., Mutillidae, *sensu stricto*), he also suggested that the prepectus pro-

vided useful information for establishing relationships.

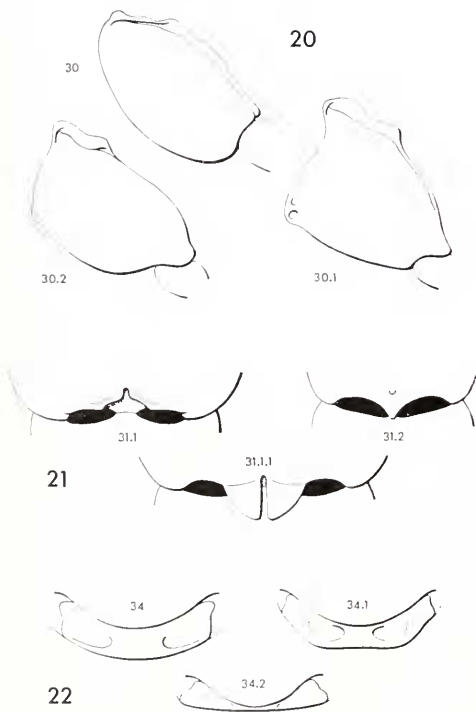
\*30. *Mesepimeron* (Fig. 20). Primitively, the mesepimeron is differentiated from the mesepisternum by a distinct pleural sulcus which is continuously distinguishable from the pleurointersegmental suture, and extends from the pleural wing process to a point just dorsal to the mesocoxa. 30.1—The pleural sulcus is indistinct or invisible over its ventral half so that the mesepimeron is not differentiated ventrally although it is apparently not reduced in size. 30.2—The pleural sulcus is coincident with the pleurointersegmental suture over its ventral half or more, so that the mese-

pimeron is reduced to a small sclerite at the posterodorsal angle of the mesopleuron.

A complete and distinct mesopleural sulcus is considered primitive because this is the condition in most non-aculeates as well as in those Aculeata considered the most primitive on the basis of other characters.

Reduction of the mesepimeron is apparently a general tendency in the more advanced Hymenoptera and is thus useful only in indicating relative position on the tree. Such a general trend cannot, however, be adequately divided into discrete states. State 30.1 has apparently been attained twice, in the mutillid and scoliid groups, and is thus of no importance in associating taxa. State 30.2 is characteristic of the apid and formicid groups and also occurs within the sphecid (e.g., *Gorytes*) and vespid (e.g., *Belonogaster*) groups. It has also arisen on internode 18-21 where it serves to associate five taxa. Its apparent weakness because of multiple origins is somewhat offset in this last instance in that some fine details of the modification are constant in these five taxa but differ from those in other groups. State 30.2 is thus considered quite good evidence for the association of the eotillid, typhoctid, chyphotid, apterogynid and bradynobaenid groups.

\*31. *Mesosternum* (Fig. 21). Primitively, the mesosternum is moderately convex and smoothly truncate posteriorly without any protuberances or carinae. 31.1—The mesosternum has a short transverse carina or dentate projection anteromesal to each coxal cavity. 31.1.1—The mesosternum has a platelike projection originating anteromesal to each coxal cavity and projecting posteriorly over it. 31.2—The mesosternum is posteriorly produced mesally, carrying the mesal points of articulation (condyles) of the mid-coxae posteriorly



FIGS. 20-22. Characters of Aculeata. 20, mesepimeron, lateral view, showing primitive and derived states of mesepimeron (30 based on *Plumarius*, ♂; 30.1 on *Arcotilla*, ♂; 30.2 on *Chyphotes*, ♂); 21, posterior region of mesosternum, ventral view, showing derived states (31.1 based on *Fedtschenkia*, ♀; 31.1.1 on *Anthobosca*, ♂; 31.2 on *Apoica*, ♂); 22, metanotum, dorsal view, showing primitive and derived states (34 based on *Anthobosca*, ♂; 34.1 on *Pseudophotopsis*, ♂; 34.2 on *Clystospenella*).

and with the anteromesal margins of the coxal cavities thus somewhat produced.

A simple mesosternum is considered primitive because this is the condition in most non-aculeate and in most aculeate Hymenoptera.

The development of a transverse carina or small tooth anterior to each mid-coxa (state 31.1) has apparently occurred on at least three occasions, on internodes 6-7 and 16-17 and in the sierolomorphid group. This is thus a rather weak state for demonstrating relationships. The further development of lamellae overlying the coxae (31.1.1) has occurred twice, on internode 7-10 (where it links six taxa) and in the rhopalosomatid group. Within the branch subtended by internode 7-10 the lamellae have been reduced to small teeth (an apparent reversal to state 31.1) in the methochid group. Nevertheless, 31.1.1 appears to provide rather good evidence for the grouping of the anthoboscid, thynnid, myzinid, tiphid, brachycistidid (and methochid) groups. The posteromesal production of the mesosternum (31.2) has apparently occurred twice, on internodes 4-5 (linking the sphecids and apids) and 19-20 (associating the scoliid and vespidae groups), although the presence of state 32.2 in the scoliids obscures this relationship.

32. *Mesocoxal contiguity*. Primitively, the mid-coxae are slightly separated basally. 32.1—The mid-coxae are contiguous as a result of a reduction in the intercoxal region of the mesosternum. 32.2—The mid-coxae are very widely separated as a result of considerable lateral expansion of the intercoxal region of the mesosternum.

Slightly separated mid-coxae are considered primitive because this is the condition in most groups of Aculeata and in particular those taxa considered most primitive on the basis of other characters.

Contiguity of the mid-coxae (32.1) has apparently arisen on at least three occa-

sions, on internodes 8-9 (in the myrmosids and mutillids) and 16-17 (linking the pompilid and rhopalosomatid groups), and in the vespidae group. It thus does not provide very strong evidence of relationships. Broad separation of the mid-coxae (32.2) has occurred twice, on internode 23-24 (female), thus associating the apterogynid and bradynobaenid groups, and in both sexes of the scoliid group. Details differ in these two occurrences of the derived state, so that the presence of 32.2 on internode 23-24 is considered strong evidence of relationship.

33. *Meso-metapleural suture*. Primitively, the meso- and metapleura articulate freely with each other. 33.1—The meso- and metapleura are closely associated and not mutually movable although not fused. 33.1.1—The meso- and metapleura are fused, at least over the dorsal half, although the suture is distinct.

Mutually movable meso- and metapleura are considered primitive because this is the condition in most non-Aculeata and most insects in general.

Immobility of the meso-metapleural suture has occurred on at least four occasions, and is an expression of the general trend toward consolidation of the mesosoma in the aculeates. State 33.1 has arisen on internodes 4-5, 12-14 and 16-18 and in the pompilid group, and is thus of little utility except in indicating approximate relative advance on the tree. The further fusion of the meso- and metapleura (33.1.1) has occurred independently in the formicid and chyphotid groups and is thus of no use in indicating relationships.

34. *Metanotum* (Fig. 22). Primitively, the metanotum is a transverse sclerite of approximately the same length mesally as laterally. 34.1—The metanotum is slightly shortened mesally so that it is only a little more than half as long mesally as laterally. 34.2—The metanotum is extremely con-

stricted mesally and reduced to a minute strip connecting the lateral areas.

A well-developed metanotum of even length is considered primitive because this is the condition in most non-aculeates (including Trigonalidae) as well as in most Aculeata.

Mesal shortening of the metanotum (34.1) has occurred at least twice, on internode 23-24 (linking the apterogynid and bradynobaenid groups, in which this state is at least partly correlated with the meso-scutellar enlargement) and in the mutillid group. It is thus not of great utility in establishing relationships. It has also occurred elsewhere, such as within the myrmosid group (e.g., *Myrmosa*). Extreme reduction of the metanotum so that the scutellum and propodeum are almost in contact (34.2) has occurred on the tree only in the scolebythid group. A similar state is present within the bethylid group (e.g., Epyrinae; Evans, 1964), however, and this may be of significance in associating these groups.

\*35. *Metapostnotum* (Fig. 23). Primitively, the metapostnotum forms a transverse groove at the anterior margin of the propodeum, being fused to the propodeum and slightly depressed. 35.1—The metapostnotum is very considerably shortened and invaginated so that it is barely visible mesally between the propodeum and the metanotum. 35.1.1—The metapostnotum is completely invaginated and not visible mesally, the propodeum being in contact with the metanotum, but the metapostnotum is still visibly continuous with the metepimeron laterally. 35.2—The metapostnotum is obscurely distinguishable laterally but merges completely with the propodeum mesally although it is apparently not invaginated. 35.3—The metapostnotum is greatly enlarged and posteriorly produced mesally, forming a "triangular area" which occupies most of the apparent disc of the propodeum. It carries the mus-

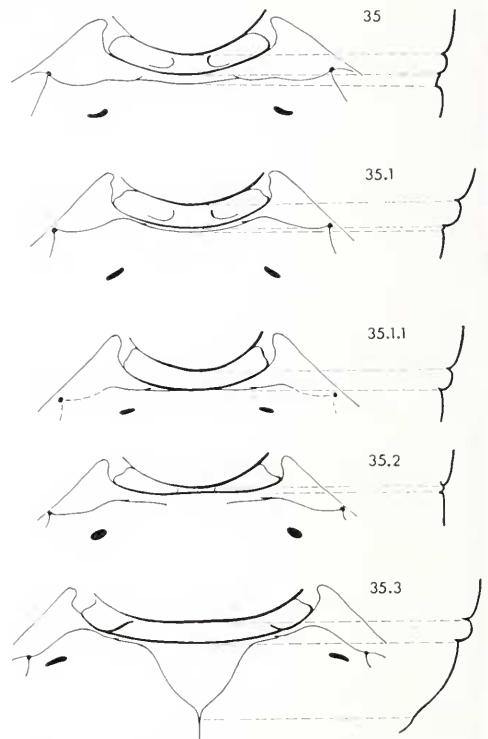


FIG. 23. Anterodorsal region of metathorax and propodeum, dorsal and lateral view (as if flattened) on left and profile on right (dorsal to right), showing primitive and derived states of metapostnotum (35 based on *Euclavelia*, ♀; 35.1 on *Anthobosca*, ♂; 35.1.1 on *Methocha*, ♂; 35.2 on *Clystopsenella*, ♀; 35.3 on *Cerceris*, ♀).

cles between the second and third phragmata to their insertion apparently far posteriorly on the propodeum.

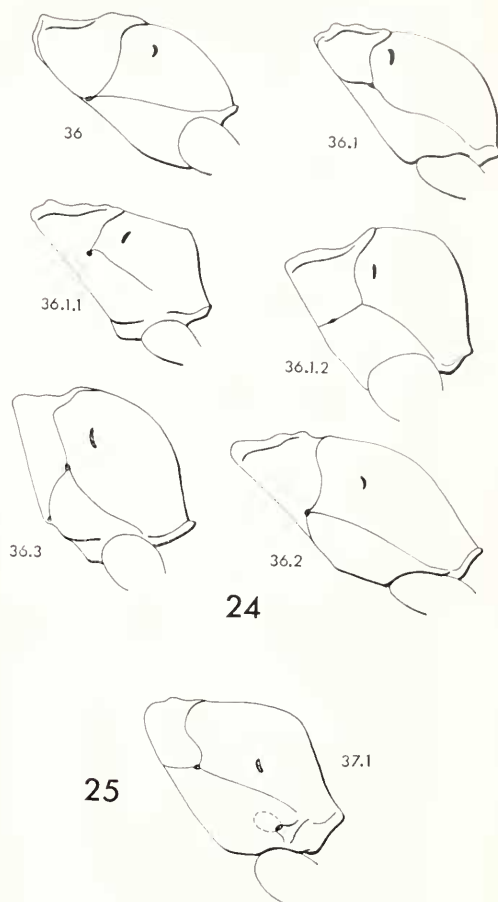
A distinct and depressed metapostnotum of approximately uniform length is considered primitive because this is the condition in many non-aculeates, especially Terebrantia (including Trigonalidae).

There is a general tendency above internode 4-6 toward shortening and invagination of the metapostnotum as part of the trend toward mesosomal consolidation. Although state 35.1 appears only once on the tree (on internode 6-7), its derivative (35.1.1) appears at least three times, in the tiphid and myzinid groups, and appar-

ently *de novo* on internode 16-18. This last derivation thus weakens the unique placement of state 35.1 somewhat, although 35.1 is logically not absolutely necessary as an antecedent to 35.1.1. State 35.2 is present in the bethylids and scolybythids, thus having arisen once (on internode 2-3) and providing useful information associating these taxa. State 35.3 is unique in the Aculeata and apparently in the Hymenoptera as a whole. This remarkable modification of the metapostnotum which is present in the sphecids and apid groups provides extremely strong evidence of the holophyletic association of these groups, having arisen on internode 4-5.

Although the various modifications of the metapostnotum need further investigation and clarification, the scheme outlined here provides useful information. In particular, the above interpretation of the origin of the "triangular area" in bees and sphecids (35.3) seems to be upheld by the arrangement of sutures (or sulci) in various sphecids (e.g., *Cerceris*) and by the placement of the muscles between the second and third phragmata (*2ph-3ph*). Daly (1964) concluded that in *Apis* the transpropodeal lines (defining the propodeal triangle) do not result from the migration of muscles *2ph-3ph* from the sides of the propodeum to the median pit, but he apparently did not consider that the propodeal triangle might represent the metapostnotum, a condition which is actually obscure in this highly evolved bee.

36. *Metapleuron* (Fig. 24). Primitively, the metepimeron is dorsally quite long, with the pleural sulcus almost or quite coincident with the meso-metapleural suture dorsal to the endophragmal pit. Below the pit the pleural sulcus is coincident with the metapleural-propodeal suture. The pit is very close to the anterior margin of the metapleuron which is constricted at this point. 36.1—The metepisternum and to a slightly lesser extent the



Figs. 24-25. Characters of Aculeata. 24, metapleuron and propodeum, lateral view, showing primitive and derived states of metapleuron (36 based on *Anthobosca*, ♂; 36.1 on *Pseudophotopsis*, ♂; 36.1.1 on *Colocistis*, ♂; 36.1.2 on *Trielis*, ♀; 36.2 on *Euclavelia*, ♀; 36.3 on *Cerceris*, ♀); 25, metapleuron and propodeum, lateral view, showing derived state of metapleural gland (37.1 composite).

metepimeron are expanded anteroventral to the endophragmal pit which is thus some distance posterior to the meso-metapleural suture. The pleural sulcus distinctly curves anterodorsally from the pit and the transepisternal groove may be visible ventrally. 36.1.1—The metepisternum and metepimeron are expanded anterior to the endophragmal pit so that the pit is some distance posterior to the meso-metapleural suture. The pleural sulcus and transepisternal suture are very indis-

tinct and barely distinguishable if distinguishable at all. 36.1.2—The metepisternum is posteriorly produced behind the endophragmal pit, in addition to slight anterior expansion of the metepisternum and metepimeron. The pleural sulcus is angulate behind the pit which is a short distance from the anterior margin of the metapleuron. 36.2—The metepimeron is expanded and somewhat produced anteroventrally so that the endophragmal pit is shifted posteriorly and the pleural sulcus is angulate. 36.3—The metepimeron is greatly expanded anteroventrally so that the pleural sulcus issues from a pit just above the mesocoxa and passes posterodorsally to the endophragmal pit.

The allocation of states for the metapleuron is that which is best correlated with the branching pattern derived from consideration of other characters, the primitive state in particular being that present in the taxa which are considered to be the most primitive on other grounds. Further investigations are needed to clarify the situation, however.

The various modifications of the metapleuron, based mainly on the position of the endophragmal pit as a marker, are somewhat equivocal and most have occurred more than once, so that they are not as strong in indicating relationships as might be expected. State 36.1 has had at least three origins, on internodes 8-9, 18-19 and 21-23. Since state 36.1.1 occurs on internode 12-14, a modification similar to 36.1 perhaps also occurred here. State 36.1.1 is also present in the bradynobaenid group. State 36.1.2 is uniquely present in the scoliid group. State 36.2 is present in the sierolomorphid, pompilid, rhopalosomatid, eotillid and typhoctid groups and thus probably arose three times (on internodes 16-17 and 21-22 and in the sierolomorphids); however, if 36.2 could have been a precursor to 36.1, then 36.2 probably arose only once, on internode 6-15. A de-

cision is, however, not possible at this stage so that 36.2 has been placed three times on the tree. State 36.3 has arisen once, on internode 4-5, and serves to associate the sphecid and apid groups strongly.

37. *Metapleural gland* (Fig. 25). Primitively, there is no gland opening to the exterior on the metapleuron. 37.1—There is a gland developed on the metapleuron and opening via a bulla and meatus just above the hind coxa.

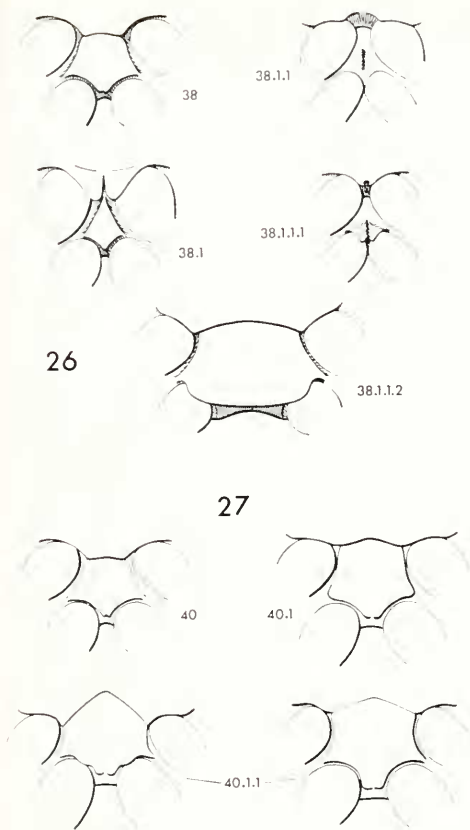
Absence of a metapleural gland is considered primitive because this is the condition in the non-aculeate Hymenoptera and in most Aculeata.

The metapleural gland is a unique feature of the formicid group and thus does not serve to indicate any groupings of the taxa considered here (see Wilson, Carpenter & Brown, 1967).

38. *Metasternum* (Fig. 26). Primitively, the mesal section of the metasternum is in approximately the same plane as the mesosternum. The metasternal area is depressed laterally to accommodate the mid-coxae, the metasternum being differentiated into approximate thirds. 38.1—The metasternum is depressed anteriorly and laterally but not completely so posteromesally, the mid-coxae being contiguous. 38.1.1—The metasternum is entirely depressed, the mid-coxae being contiguous. 38.1.1.1—The metasternum is entirely depressed but small teeth are developed just anterior to the metacoxal cavities, the mid-coxae being contiguous. 38.1.1.2—The metasternum is entirely flat and broad but not depressed, being at the same level as the mesosternum, with the mid-coxae widely separated.

A metasternum with only the lateral thirds depressed is considered primitive because this is the condition in various aculeates that are considered to be the most primitive on the basis of other characters.

Although state 38.1 has apparently



Figs. 26-27. Characters of Aculeata. 26, posterior region of mesosoma, ventral view, showing primitive and derived states of metasternum (38 based on *Pristocera*, ♂; 38.1 on *Anthobosca*, ♀; 38.1.1 on *Fedtschenkia*, ♀; 38.1.1.1 on *Pseudophotopsis*, ♂; 38.1.1.2 on *Trielis*, ♀); 27, posterior region of mesosoma, ventral view, showing primitive and derived states of metasternal anterior production (40 based on *Pristocera*, ♂; 40.1 on *Typhoctoides*, ♀; 40.1.1 on *Apterogynia*, ♀, and *Bradynobaenus*, ♂, left to right).

arisen only twice (on internode 4-6 and in the plumariid group), its presumed utility is diminished by the frequent additional modifications of the metasternum. Thus, 38.1.1 has arisen three times, on internodes 7-8 and 6-15, and in the plumariid group (male), and has apparently been reversed on internode 18-21. State 38.1.1.1 is uniquely characteristic of the mutillid group and 38.1.1.2 is present in the scoliids only, so that these two states are of no use in grouping the taxa.

39. *Metasternal differentiation*. Primitively, the meso- and metasterna are clearly differentiated by a definite discontinuity in the form of a deep sulcus or difference in level. 39.1—The meso- and metasterna are barely differentiated because of fusion and loss of any definite sulcus, especially mesally.

Well-differentiated meso- and metasterna are considered primitive because this is the condition in most non-aculeates as well as in most Aculeata.

Loss of differentiation of the metasternum is most probably another expression of the general tendency toward consolidation of the mesosoma. It has occurred at least three times, on internodes 4-5 and 18-21 and in the scoliid group, so that it is of little use in establishing relationships.

\*40. *Metasternal anterior production* (Fig. 27). Primitively, the metasternum has the anterior margin approximately straight. 40.1—The metasternum is slightly anteriorly produced mesally between the mid-coxae so that its anterior margin attains the level of the anterior extremities of the mid-coxae. 40.1.1—The anterior margin of the metasternum is anteriorly produced mesally and reaches a point anterior to the level of the anterior extremities of the mid-coxae.

A metasternum with approximately straight anterior margin is considered primitive because this is the condition in most non-Aculeata as well as in most aculeates.

Anterior production of the metasternum has taken place in only one line, providing good evidence of the holophyletic relationship of the cotillid, typhoctid, chyphotid, apterogynid, and bradynobaenid groups. State 40.1 has arisen on internode 18-21, and its derivative (40.1.1) reinforces the association of the apterogynids and bradynobaenids, appearing on internode 23-24.

41. *Metacoxal contiguity*. Primitively, the metacoxae are nearly or actually contiguous. 41.1—The metacoxae are broadly separated as a result of lateral expansion of the intercoxal region of the metasternum.

Contiguous metacoxae are considered primitive because this is the condition in most non-aculeate and in most aculeate Hymenoptera.

The derived state is characteristic of the scoliid group only, and is thus of no importance in the derivation of higher groupings.

42. *Metathoracic-propodeal pleural suture*. Primitively, the metathoracic-propodeal intersegmental pleural suture is clearly discernible over its entire length, both dorsal and ventral to the endophragmal pit. 42.1—The metathoracic-propodeal pleural suture is completely obliterated ventral to the endophragmal pit but is distinct dorsally. 42.1.1—The metathoracic-propodeal pleural suture is completely obliterated, both dorsal and ventral to the endophragmal pit.

A completely discernible metathoracic-propodeal pleural suture is considered primitive because this is the condition in most non-aculeates.

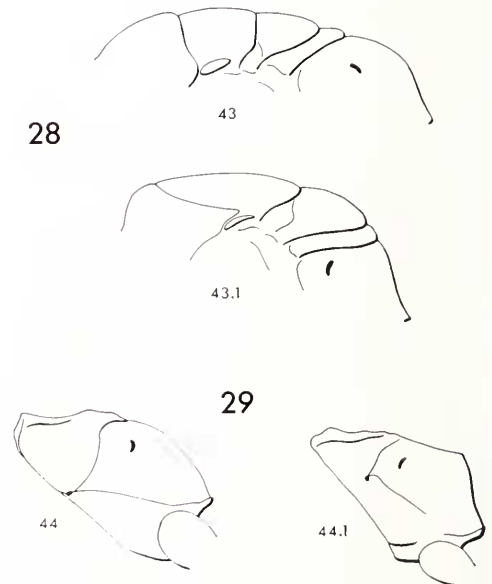
The obliteration of the metathoracic-propodeal pleural suture has occurred on numerous occasions and this character is thus almost valueless for determining higher groupings. State 42.1 has apparently arisen on six occasions, on internodes 1-2, 12-14 and 18-21, and in the apid, methochid and sierolomorphid groups. State 42.1.1 has occurred twice, in the tibiid group and (apparently *de novo*) on internode 8-9. The placement of this state on internode 8-9 is especially interesting in the light of Krombein's (1940) statement that a major difference between the "Myrmosinae" and "Mutillidae" lay in the complete absence of this intersegmental suture in the myrmosids and its presence in the

mutillids. It actually appears that the suture is completely obliterated in both, but in some of the more highly developed mutillids there is a secondary development of a weak carina along the apparent line of this suture. State 42.1.1 is thus a condition linking the myrmosid and mutillid groups, rather than one differentiating them.

43. *Propodeal length* (Fig. 28). Primitively, the propodeum is of moderate length, being at least as long as high. 43.1—The propodeum is much shortened in its entirety but especially dorsally, so that the metanotum extends posteriorly to a point almost perpendicularly above the base of the metasoma.

A propodeum of moderate dorsal length is considered primitive because this is the condition in most non-aculeates as well as in most aculeates.

The shortening of the propodeum may



Figs. 28-29. Characters of Aculeata. 28, dorsal region of mesosoma, lateral view, showing primitive and derived states of propodeal length (43 based on *Anthobosca*, ♀; 43.1 on *Ceramius*, ♀, modified); 29, metapleuron and propodeum, lateral view, showing primitive and derived states of discal distinction (44 based on *Anthobosca*, ♂; 44.1 on *Colocistis*, ♂).



be another expression of the general tendency toward consolidation of the mesosoma. State 43.1 has occurred twice, the mechanism differing slightly in detail, in the vespid and bradynobaenid groups. It is thus of no use in the derivation of higher groupings.

44. *Discal distinction* (Fig. 29). Primitively, the disc and declivity of the propodeum are not distinct but merge gradually into each other. 44.1—The disc and declivity form distinct dorsal and posterior surfaces, often separated by a carina.

A propodeum with merging disc and declivity is considered primitive because this is the condition in most non-aculeates as well as in most members of the Aculeata.

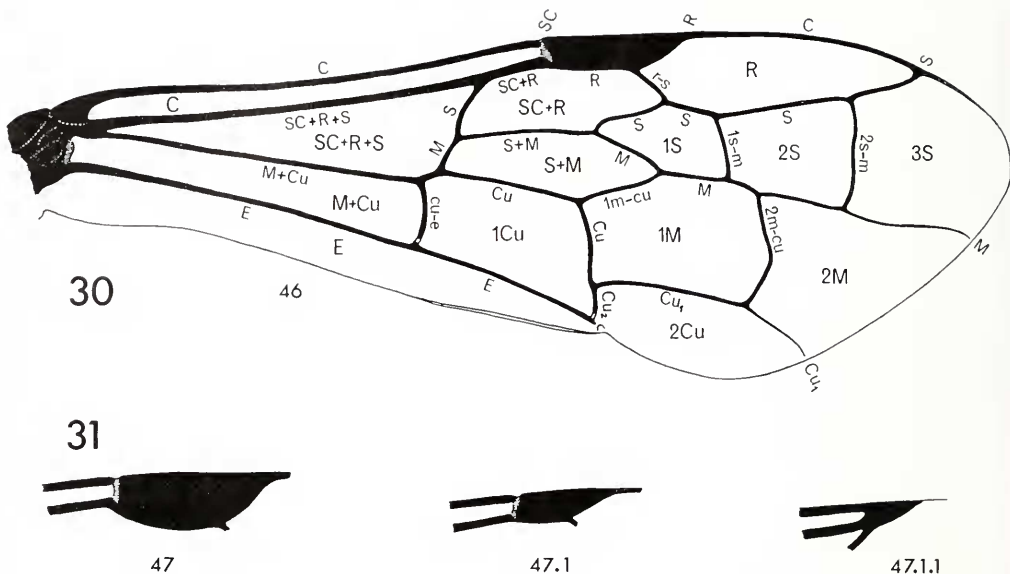
The degree of distinctness between the disc and declivity is difficult to quantify. State 44.1 is considered to be fully developed when the two surfaces involved are almost perpendicular to one another. Such a condition has arisen on at least three occasions, on internode 12-14 (linking the tiphiid and brachycistidid groups) and in the bradynobaenid and scoliid groups. Since this state is approached in many other instances, its presence is not a good indicator of higher groupings.

\*45. *Extent of forewing venation*. Primitively, the longitudinal veins of the forewing attain the apical margin of the wing membrane. 45.1—The venation of the forewing is reduced or retracted so that the veins extend into the apical half of the wing membrane but do not reach the margin. 45.1.1—The venation of the forewing is extremely reduced so that it does not extend beyond the basal half of the wing membrane.

Venation which attains the apical margin of the wing membrane is considered primitive because this is the condition in most Symphyta and many Terebrantia (including Trigonalidae).

Retraction of the venation from the apex of the wing membrane is extremely common, and state 45.1 has apparently occurred on at least nine occasions, on internodes 1-2, 12-14 and 18-21, and in the apid, mutillid, anthoboscid (female), sierolomorphid, rhopalosomatid and scoliid groups. This state is thus of little utility in determining relationships. The extreme reduction of venation in relatively large individuals without an associated tendency toward brachyptery is apparently present in only the apterogynid and bradynobaenid groups (on internode 23-24, state 45.1.1) and is thus considered quite good evidence of their relationship. There are, however, some members of the myzinid group which show a somewhat similar reduction in venation but with an accompanying decrease in wing or body size (e.g., "*Meria*" *infradentata*; *Myzinella patrizii*, Guiglia, 1968).

\*46. *Cells of forewing* (Fig. 30). Primitively, there are ten closed cells in the forewing, viz., C, SC+R+S, SC+R, R, 1S, 2S, S+M, 1M, M+Cu, 1Cu. 46.1—There are eight closed cells in the forewing, viz., C, SC+R+S, SC+R, R, 1S, S+M, M+Cu, 1Cu. 46.1.1—There are seven closed cells in the forewing, viz., C, SC+R+S, SC+R, R, S+M, M+Cu, 1Cu. 46.1.1.1—There are six closed cells in the forewing, viz., C, SC+R+S, SC+R, R, S+M, M+Cu. 46.2—There are seven closed cells in the forewing, viz., C, SC+R+S, (SC+R)+1S, R, S+M, M+Cu, 1Cu. 46.3—There are nine closed cells in the forewing, viz., C, SC+R+S, R, (SC+R)+1S, 2S, S+M, 1M, M+Cu, 1Cu; vein S is obliterated proximal to its fusion with r-s. 46.4—There are nine closed cells in the forewing, viz., C, SC+R+S, R, (SC+R)+1S, 2S, S+M, 1M, M+Cu, 1Cu; vein S is obliterated just distal to its separation from vein M. 46.5—There are five closed cells in the forewing, viz., C, SC+R+S, SC+R, M+Cu, 1Cu. 46.5.1—



FIGS. 30-31. Characters of Aculeata. 30, forewing, showing primitive state of cells; veins (smaller letters) are: C = costa, Cu = cubitus, E = empusula, M = media, R = radius, S = sector, SC = subcosta (46 based on *Anthobosca*, ♂); 31, pterostigma, showing primitive and derived states of its size (47 based on *Anthobosca*, ♀; 47.1 on *Chirodamnus*, ♀; 47.1.1 on *Apterygyna*, ♂).

There are three closed cells in the forewing, viz., C, SC+R+S, M+Cu.

Ten closed cells is considered the primitive condition because this is the state in the Trigonalidae and also in many aculeate taxa which are considered relatively primitive on the basis of other characters. The trend has apparently been toward reduction in cell number in the Terebrantia, and ten is the maximal number of cells found in the aculeates.

Losses of various veins and thus reductions in the number of cells have been quite common although most appear to be characteristic of single taxa only and are thus of no use in establishing groupings. State 46.1 has arisen at least three times, on internode 1-2 and in the rhopalosomatid and formicid groups, as well as within many of the other groups. State 46.1.1 is present on internode 2-3, and 46.1.1.1 is characteristic of the scolebythid group and also some species within the bethylid group (e.g., *Lytopsenella*; Evans, 1964). State 46.2 appears in the sierolomor-

phids; 46.3 is developed in the methochiid group; 46.4 is present in the tiphiids. State 46.5 has apparently arisen on internode 23-24, linking the apterogynid and bradynobaenid groups, with its derivative (46.5.1) being present in the bradynobaenids; these last states are very characteristic and considered good evidence of this relationship.

47. *Pterostigmal size* (Fig. 31). Primitively, the pterostigma is large and prominent. 47.1—The pterostigma is reduced although nevertheless distinct and is moderate to small in size. 47.1.1—The pterostigma appears as a mere swelling in the venation, and is thus very small.

A large pterostigma is considered primitive because this is the condition in most non-aculeates and in many aculeates which are considered relatively primitive on the basis of other characters.

There appears to be a tendency towards reduction in the size of the pterostigma in various of the more highly developed

groups. Thus, state 47.1 has apparently occurred on at least two occasions, on internodes 4-5 and 15-16. This trend has been reversed, however, in the eotillid and chyphotid groups, where the apparent primitive state is present. Extreme reduction (47.1.1) is characteristic of the apterogynid and bradynobaenid groups, and has thus developed on internode 23-24; it also occurs within the sphecid (e.g., *Zyzzyx*) and apid (e.g., *Apis*) groups. These states are thus not considered to provide good evidence of relationships.

48. *Pterostigmal sclerotization*. Primitively, the pterostigma is heavily sclerotized and uniformly thickened. 48.1—The sclerotization of the pterostigma is reduced so that the pterostigma appears to be bounded by a distinct vein, although some sclerotization of the cell so formed is generally retained.

A heavily sclerotized pterostigma is considered primitive because this is the condition in many non-aculeates as well as in most Aculeata.

Reduction of pterostigmal sclerotization has occurred at least twice, on internodes 16-17 (associating the pompilid and rhopalosomatid groups) and 19-20 (linking the vespids and scoliids) as well as within various other groups such as the mutillids (e.g., *Mutilla*) and sphecids (e.g., *Pseudoplisus*). This character is thus only of use in confirming the indications of relationships provided by other characters.

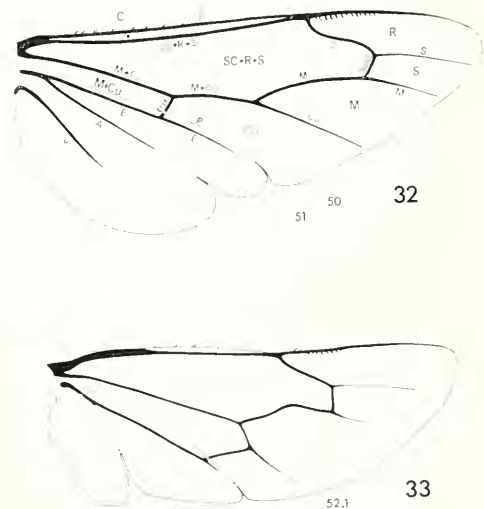
49. *Extent of hind wing venation*. Primitively, the longitudinal veins of the hind wing attain the apical margin of the wing membrane. 49.1—The venation of the hind wing is retracted or reduced so that the veins extend into the apical half of the wing membrane but do not attain the margin. 49.1.1—The venation of the hind wing is greatly reduced and restricted to the basal half of the wing membrane.

Venation which attains the apical mar-

gin of the wing membrane is considered primitive because this is the condition in most Symphyta and many Terebrantia (including Trigonalidae).

Retraction of the veins away from the apical margin of the hind wing has occurred on numerous occasions, as with the forewing, although the pattern of derivations is not identical for both wings. State 49.1 is present on internodes 2-3, 12-14 and 18-21, and in the mutillid, sierolomorphid, rhopalosomatid and scoliid groups, as well as within various other groups. State 49.1.1 has occurred on internode 23-24 and in the scolebythid group, as well as within the bethylid group (e.g., *Pristocera*). This character is thus of minimal utility in determining relationships.

50. *Cells of hind wing* (Fig. 32). Primitively, there are three closed cells in the hind wing, viz., C, SC+R+S, M+Cu. 50.1—There are two closed cells in the hind wing, viz., SC+R+S, M+Cu; vein C is reduced distally. 50.2—There are two closed cells in the hind wing, viz., C,



FIGS. 32-33. Characters of Aculeata. 32, hind wing, showing primitive state of cells and veins; veins as in forewing, plus A = anal, J = jugal bar, P = apical fold (50, 51 based on *Prionyx*, modified); 33, hind wing, showing derived state of crossvein cu-c (52.1 based on *Anthobosca*, ♂).

(SC+R+S)+(M+Cu); vein M+Cu is obliterated. 50.3—There is one closed cell in the hind wing, viz., C; vein M+Cu and all cross-veins are obliterated. 50.3.1—There are no closed cells in the hind wing.

Three closed cells is considered the primitive condition because this is the maximum number of cells found in the Aculeata. In the Terebrantia the trend has apparently been toward reduction in cell number.

The distal reduction of the costal vein (state 50.1) has occurred on numerous occasions, on internodes 7-8 and 16-17, as well as in the apid, methochid, sierolomorphid, formicid, eotillid and chyphotid groups. This state is thus of no use as an indicator of higher groupings. State 50.2 is uniquely present in the bradynobaenid group. State 50.3 is present in the bethylid group, and its derivative (50.3.1) is present in the scoblebythids as well as within the bethylid group (e.g., *Pristocera*), so that this modification is probably significant in associating these groups.

\*51. *Hind wing anal and jugal veins* (Fig. 32). Primitively, one anal vein and a veinlike jugal bar are present in the hind wing, i.e., veins A and J are present. 51.1—An anal vein is present in the hind wing but vein J is obliterated. 51.2—Both veins A and J are obliterated in the hind wing.

The presence of both an anal vein and a jugal bar is considered primitive because this is the maximal number of such veins found in the Aculeata. In the non-aculeates the trend has been toward loss of these veins; they are generally both absent in Terebrantia, including Trigonalidae, but are present in the most primitive Symphyta (e.g., Xyelidae). Although the jugal "vein" is not a true vein, but rather a development from the jugal bar (Hamilton, 1972a), as shown by its position in the jugal lobe, it is most convenient to

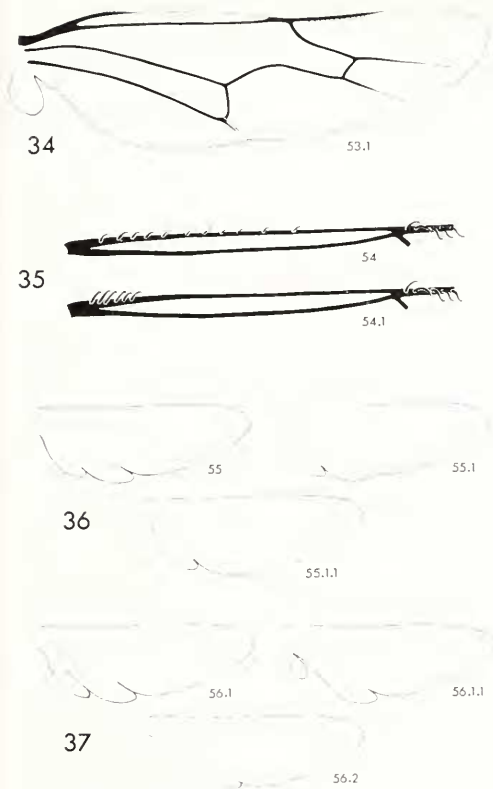
treat it in the same way as the true veins for reference purposes.

Both the anal and jugal veins are retained in only the sphecid group and the anal vein only is retained in the apid group, which is thus characterized by state 51.1. Both veins have apparently been lost in all other groups, so that state 51.2 has arisen on internodes 1-2 and 4-6, as well as within the sphecid (most species, but both veins present in *Sphex*, *Prionyx*, e.g.) and apid (e.g., *Megachile*, *Mesochaira*) groups. Vein A has apparently reappeared as a minute spur within the anthoboscid (e.g., *Anthobosca* sp. male) and thynnid (e.g., *Hemithynnus*) groups, although its origin on vein E is shown as a basal thickening of that vein in many other groups. This character is thus only useful in so far as it emphasizes the presence of a very primitive state in a taxon (the sphecids) otherwise considered highly derived, thus indicating a remote separation of the sphecid (and apid) line from the other aculeates.

52. *Hind wing cross-vein cu-e* (Fig. 33). Primitively, in the hind wing cross-vein cu-e originates basal to the point of separation of veins M and Cu. 52.1—Cross-vein cu-e originates distal to the point of separation of veins M and Cu.

A basal position for cross-vein cu-e is considered primitive because this is the condition in most taxa of Aculeata. In taxa showing both states, state 52.1 generally occurs in those members considered most derived on the basis of other characters.

Although state 52.1 appears on the tree only once (on internode 6-7) and thus seems to provide good evidence of the relationship of nine mutilloid and tiphoid taxa, its strength is considerably diminished by its presence within various other taxa such as the sphecids (e.g., *Gorytes*) and vespids (e.g., *Synoeca*). There have also rarely been apparent reversals to the



FIGS. 34-37. Characters of Aculeata. 34, hind wing, showing derived state of vein Cu (53.1 based on *Myrmosa*, ♂); 35, anterior basal region of hind wing, showing primitive and derived states of basal hamuli (54 based on sphecid; 54.1 on pompilid); 36, hind wing, showing primitive and derived states of plical lobe (all composite); 37, hind wing, showing derived states of jugal lobe (all composite).

primitive state, within the myzinid and tiphiid groups (some females, e.g., *Myzinum*, *Tiphia*).

\*53. *Hind wing vein Cu* (Fig. 34). Primatively, vein Cu is distinctly present in the hind wing distal to its point of separation from vein M. 53.1—Vein Cu is obliterated distal to its separation from vein M.

Presence of vein Cu distally is considered primitive because this is the condition in most non-aculeate and in most aculeate Hymenoptera.

The loss of the free section of vein Cu has apparently occurred on a single occasion, on internode 7-8, thus strongly asso-

ciating the sapygid, myrmosid and mutillid groups. There is some confusion regarding the mutillids, however. The mutillid genus with the greatest proportion of primitive character states (*Pseudophotopsis*) has a condition like state 53.1, but the more derived members often seem to show the primitive state (e.g., *Tricholabiodes*). Such a direct reversal is logically unlikely, since it involves the regaining of a lost structure. The mutillids commonly have the venation of the hind wing considerably modified, however, various veins or sections of them being lost or suppressed so that there are no closed cells. Such modification could conceivably have caused the apparent redevelopment of a free spur in the position of vein Cu, perhaps actually as a result of a break in and displacement of vein E.

54. *Basal hamuli* (Fig. 35). Primatively, the basal hamuli are dispersed along the costal margin (on vein C) of the hind wing distal to the point of separation of veins C and SC+R+S. 54.1—The basal hamuli are concentrated into a basal cluster approximately at the point of separation of veins C and SC+R+S. 54.2—The basal hamuli are completely absent.

A dispersed series of basal hamuli is considered primitive because this is the condition in the Trigonalidae as well as in those Aculeata judged to be most primitive on the basis of other characters. Lanham (1951) considered the Braconidae (Terebrantia) to have a very primitive condition, merely bearing a dispersed series of strong, straight bristles. By contrast, Rasnitsyn (1969) showed both a basal cluster and a dispersed series in his putative generalized symphytan.

State 54.1 has occurred on two occasions, apparently, on internodes 8-9 and 15-16. State 54.2 is present on internodes 18-19 and 23-24 and in the brachycistidid group, as well as within others such as the mutillid group (most species, except *Pseu-*

*dophotopsis*) so that these states are useful only as confirmatory indicators rather than prime establishers of relationships.

55. *Plical lobe* (Fig. 36). Primitively, the plical lobe is indicated by a moderate incision of the hind margin of the hind wing. 55.1—The plical lobe is indicated by a shallow notch in the hind margin of the wing. 55.1.1—The plical lobe is not indicated by any modification of the margin of the wing although the plical furrow indicates its extent within the wing membrane.

A plical lobe indicated by a moderate incision is considered primitive because this is the condition in those Aculeata judged to be most primitive on the basis of other characters. As Hamilton (1971) has pointed out, the jugal and vannal folds are alternative mechanisms of wing folding and thus are mutually exclusive; the presence of both jugal and vannal lobes in the same wing is thus impossible. In Hymenoptera there is no true vannal fold, the anterior margin of the supposed "vannal" lobe being formed by the plical furrow. This lobe may thus conveniently be called the "plical lobe" to maintain morphological consistency.

Modification of the depth of the notch indicating the plical lobe has apparently occurred a number of times. Thus state 55.1 has arisen on at least three occasions, on internodes 7-8 and 6-15 and in the thynnid group; 55.1.1 has developed twice, on internode 18-21 and in the scoliid group. An apparently primitive state has, however, been redeveloped in both the rhopalosomatid and eotillid groups independently, and the condition varies within many of the taxa, so that this character is not of fundamental value in indicating groupings.

\*56. *Jugal lobe* (Fig. 37). Primitively, the jugal lobe is long, being indicated by a slight notch in the margin of the hind

wing. 56.1—The jugal lobe is moderately long and indicated by an axillary incision which extends about half the anterior length of the lobe. 56.1.1—The jugal lobe is small and indicated by a well-developed axillary incision which extends almost to the base of the hind wing. 56.2—The jugal lobe is absent.

A long jugal lobe indicated by a notch is considered primitive because this is the condition in most Symphyta and also in the more generalized members of a few taxa of Aculeata judged to be relatively primitive on the basis of other characters (especially of the wings). The Terebrantia have generally lost this lobe and so do not provide any useful information relative to this character.

The development of a marked incision (56.1) has apparently occurred only once on the tree, on internode 4-6, although it is also present within the sphecid (e.g., *Philanthus*) and apid (e.g., *Megachile*) groups. State 56.1.1 has also arisen on the tree only once, on internode 7-8, associating the sapygids, myrmosids and mutillids, although a similar tendency is rarely present within the sphecids (e.g., *Trypargilum*). By contrast, complete absence of the jugal lobe (56.2) has occurred at least three times, on internode 1-2 (associating the plumariids, bethylids and scolebythids) and in the sierolomorphid and typhoctid groups. This state is also present within the mutillid group (all members except *Pseudophotopsis*). Despite the fact that these states are somewhat equivocal, this character seems to provide useful information on groupings.

57. *Leg form* (Fig. 38). Primitively, the legs are relatively slender and of generalized form, all three pairs being similar. 57.1—The legs have the femora and tibiae expanded to some degree so that they are rather stout, especially the middle and hind pairs. 57.2—The legs have only the femora much inflated. 57.3—The legs have

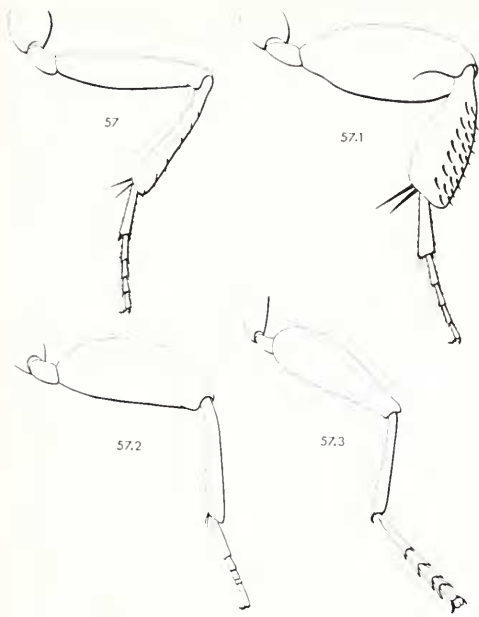


FIG. 38. Leg, showing primitive and derived states of leg form (57 based on *Anthobosca*, ♂, hind leg; 57.1 on *Anthobosca*, ♀, hind leg; 57.2 on *Clystoscenella*, ♀, hind leg; 57.3 on *Olixon*, ♀, front leg).

the tarsi expanded and flattened and the fore-tibiae swollen.

Slender, unspecialized legs are considered primitive because this is the condition in most non-aculeates as well as in most Aculeata.

Modifications of the legs have occurred numerous times, often being correlated with burrowing or prey manipulation. State 57.1 has arisen on at least four occasions, always only in females, on internodes 7-10 and 21-23, and in the plumariid and scoliid groups. The legs have reverted to a slender condition in the methochid group and within the myzinid (e.g., *Pterombrus*) and thynnid (e.g., *Diamma*) groups, so that this state is additionally weakened as an indicator of relationships. State 57.2 is uniquely characteristic of both sexes of the scolebythid group, and 57.3 is present in only the females of the rhopalosomatid group (and is of some importance here since it associates *Rhopa-*

*losoma* and *Olixon*, the latter genus having been placed elsewhere on occasion—e.g., in the Pompilidae, by Reid, 1939).

58. *Arolium*. Primitively, each arolium forms a well-developed pad between the tarsal claws. 58.1—The arolium is completely reduced and absent, or at least not distinguishable under a magnification of 100×.

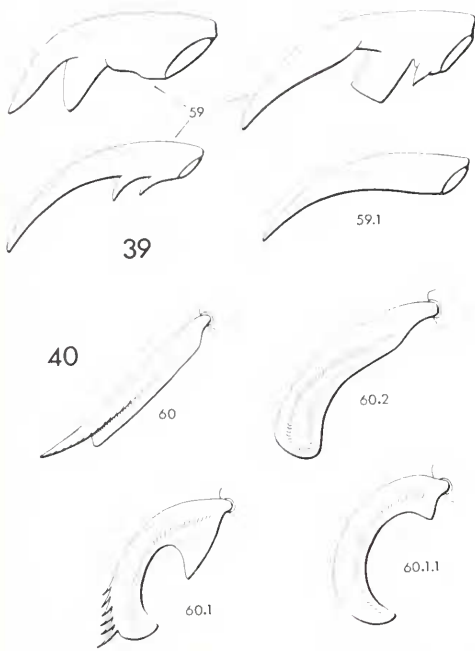
A well-developed arolium is considered primitive because this is the condition in most non-aculeate and aculeate Hymenoptera as well as the Insecta in general.

The arolium has been lost on a number of occasions, in the females of the myrmosid group, both sexes of the eotillids and in the female on internode 21-23 and the male on internode 23-24, so that the chyphotids possess arolia in males only (although much reduced in some males in the subgenus *Pitanta*, e.g., *Chyphotes mojave*; Mickel, 1967), and the apterogynids and bradynobaenids lack them in both sexes. Loss or extreme reduction of the arolium has also occurred within the apids (e.g., *Megachile*) at least. Because of its multiple occurrences this state is not a good indicator of groupings.

59. *Claws* (Fig. 39). Primitively, each claw bears one or more processes on the ventral margin, these forming teeth or producing a cleft appearance; in either case the claw is referred to as "toothed." 59.1—Each claw is simple, with a smooth ventral margin and no trace of any tooth.

Toothed claws are considered primitive because this is the condition in many non-aculeates (including Trigonalidae) and in many Aculeata considered relatively primitive on the basis of other characters.

The loss of teeth on the tarsal claws has occurred on numerous occasions. State 59.1 is characteristic of the entire brachycystidid, scoliid and bradynobaenid groups and the females of the plumariid and myrmosid groups. It has also occurred within the bethylids (e.g., *Chrysis*), mutil-



FIGS. 39-40. Characters of Aculeata. 39, claw, showing primitive and derived states (59 based on *Anthobosca*, ♀, *Apterogyna*, ♂, and *Sphex*, ♀, left to right then below; 59.1 on *Bradynobaenus*, ♀); 40, foretibial calcar, posterior view, showing primitive and derived states (60 based on *Anthobosca*, ♂; 60.1 on *Apterogyna*, ♂; 60.1.1 on *Bradynobaenus*, ♀; 60.2 on *Triclis*, ♂).

lids (all except *Pseudophotopsis*), cotillids (e.g., *Eotilla*), typhoctids (e.g., *Typhoctoides*), sphecid (e.g., *Bembix*) and apids (e.g., *Megachile*) at least. The primitive state also covers a variety of forms of teeth which cannot readily be separated into distinct states, some of which may even be secondary derivations (see the section on the mutillids below for a discussion of *Rhopalomutilla*). This character is thus very weak and of essentially no significance in determining relationships.

\*60. *Foretibial calcar* (Fig. 40). Primatively, the single calcar of the foretibia is approximately straight with an elongate inner lamina which may be somewhat shortened. 60.1—The foretibial calcar is strongly curved inward and is more or less even in width but with a small outer

spine present at the apex. 60.1.1—The foretibial calcar is strongly curved inward and is more or less even in width with the apex obtuse. 60.2—The foretibial calcar is inwardly curved, spatulate at the apex and hollowed along the posterior surface.

An approximately straight calcar is considered primitive because this is the condition in most non-Aculeata as well as in most aculeates.

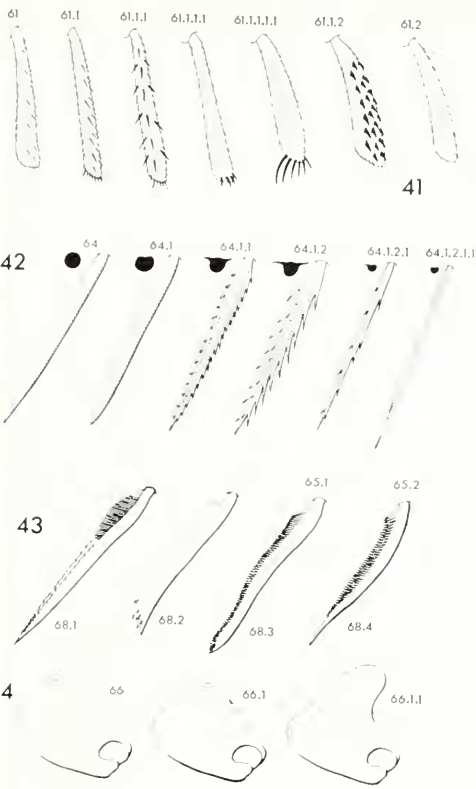
There is actually greater variation in the foretibial calcar than would appear from the above. The primitive state covers many rather subtle variations which could not unequivocally be divided into separate states. Further, 60.1, 60.1.1 and 60.2 are actually quite similar and it is thus possible that they should really be considered as expressions of the same series. Nevertheless, 60.1 (apterogynids) and its derivative, 60.1.1 (bradynobaenids) do serve to associate the groups subtended by internode 23-24, as has previously been noted by Reid (1941). State 60.2 characterizes the scoliid group.

61. *Middle tibial spines* (Fig. 41). Primatively, each middle tibia bears many scattered setae, a few of which are slightly stronger than the remainder and are termed "spiniform." 61.1—Each middle tibia bears scattered spiniform setae which are readily identifiable as weak spines. 61.1.1—Each middle tibia bears scattered spines which are fairly strong and are termed "moderate." 61.1.1.1—Each middle tibia bears moderate spines which are absent basally and present only apically. 61.1.1.1.1—Each middle tibia bears very strong spines apically only. 61.1.2—Each middle tibia bears scattered spines which are extremely strong and prominent. 61.2—Each middle tibia is completely spineless and bears only a few weak setae.

An essentially spineless but setose middle tibia is considered primitive because this is the condition in most non-aculeates.

The tibial spines are very variable





Figs. 41-44. Characters of Aculeata. 41, middle tibia, showing primitive and derived states of spines (61 based on *Pristocera*, ♂; 61.1 on *Plumarius*, ♂; 61.1.1 on *Anoplius*, ♀; 61.1.1.1 on *Paraponera*, ♀; 61.1.1.1.1 on *Bradynobaenus*, ♂; 61.1.2 on *Trichlis*, ♀; 61.2 on *Clystopenella*, ♀); 42, middle tibial spur, cross section and dorsal view, showing primitive and derived states (64, 64.1, 64.1.1 composite; 64.1.2 based on *Apterogyna*, ♂; 64.1.2.1 on *Bradynobaenus*, ♂, hind spur; 64.1.2.1.1 on *Bradynobaenus*, ♀, hind spur); 43, middle or hind tibial spur, showing derived states of calcaria (65.1, 68.3 based on *Paraponera*, ♀; 65.2, 68.4 on *Methocha*, ♀; 68.1 on *Pepsis*, ♀; 68.2 on *Euparagia*, ♀); 44, hind coxa, showing primitive and derived states (66 based on *Anthobosca*, ♂; 66.1 on *Sicrolomorpha*, ♂; 66.1.1 on *Myrmosa*, ♂).

within and among taxa and the states described are somewhat equivocal so that assignment of the various states to the different taxa is sometimes almost arbitrary. This character is thus of minimal use in determining relationships. State 61.1 has apparently arisen on internode 1-4 and in the plumariid group, some development of tibial spines being charac-

teristic of almost all aculeates. State 61.1.1 has developed on internodes 6-7 and 21-23, and in the sphecid, pompilid and typhoctid groups as well as female plumariids. The spines have been somewhat reduced in the methochid group, however, so that it is assigned state 61.1. State 61.1.1.1 has developed in the formicid group and also on internode 23-24, while its derivative, 61.1.1.1.1, is present in the bradynobaenids. State 61.1.2 is present only in the scoliids. Complete loss of spines (61.2) has taken place only in the scolebythid group.

62. *Hind tibial spines* (Fig. 41). The allocation of states for the hind tibial spines is as for the middle tibia (character 61).

The same comments apply to the hind tibial spines as to those of the middle legs. The allocation of states is similar except that 62.1.1 is not present in female plumariids and 62.1.1.1 is developed on internode 21-23, being present in the chyphotid group. Because of these differences, this character is not considered to duplicate the previous one.

63. *Middle tibial spur number*. Primatively, each mid-tibia bears two spurs apically. 63.1—Each mid-tibia bears one spur apically. 63.2—Each mid-tibia bears no spurs apically.

A middle tibia with two spurs is considered primitive because this is the condition in most non-Aculeata and also in most aculeates.

The loss of middle tibial spurs has occurred on a number of occasions, each time in a single taxon, so that this character is of no use in establishing relationships. State 63.1 is present in the apid, methochid (female only), brachycistidid and scoliid groups, and 63.2 has arisen in the bradynobaenids. One spur has also been lost within various other taxa such as the bethylid (e.g., *Deinodryinus*), mutillid (e.g., *Acanthophotopsis*) and sphecid

(e.g., *Larra*, *Zyzzya*) groups, and both spurs have been lost within the formicid group (e.g., *Crematogaster*).

64. *Basic form of middle and hind tibial spurs* (Fig. 42). Primitively, each spur is simple and approximately circular in cross-section, forming a very narrow cone. 64.1—Each tibial spur is slightly flattened dorsally but retains simple margins. 64.1.1—Each tibial spur is dorsally flattened and has serrate margins. 64.1.2—Each tibial spur is dorsally flattened and with deeply dentate margins. 64.1.2.1—Each tibial spur is dorsally flattened and somewhat elongated, with a few teeth on the margins. 64.1.2.1.1—Each tibial spur is dorsally flattened and threadlike (nematiform) with simple margins.

Conical tibial spurs are considered primitive because this is the condition in many non-Aculeata, particularly Terebrantia, and in those aculeates considered relatively primitive on the basis of other characters.

Although the modifications of spur form have occurred on various occasions, there does seem to be a logical progression in the pattern shown in at least the chyphotid, apterogynid and bradynobaenid groups which serves to associate them. State 64.1 is present in females only on internodes 6-7 and 21-23, and in both sexes of the pompilid and scoliid groups. 64.1.1 has arisen in females on internode 7-8 and in both sexes on internode 4-5. State 64.1.2 is present in both sexes on internode 23-24, and its modification (64.1.2.1) occurs in the males of bradynobaenids while the females of that taxon are even more modified and exhibit state 64.1.2.1.1.

65. *Middle tibial calcar* (Fig. 43). Primitively, the mid-tibial spurs are similar, showing no signs of modification as calcaria. 65.1—The inner spur of the mid-tibia is modified as a calcar by formation of a dorsal pectinate carina. 65.2—The

(inner?) spur of the mid-tibia is modified as a calcar by the development of dorsal pectination but without carina formation.

Unmodified spurs are considered primitive because this is the condition in most Hymenoptera, both non-aculeates and aculeates.

The formation of a calcar on the middle tibia is uncommon and has occurred twice, each time in a slightly different fashion. State 65.2 is present only in the females of the methochid group and 65.1 occurs in both sexes of the formicids, although the modification is minimal in some (e.g., *Camponotus*). This character is therefore of no use in establishing higher groups.

66. *Form of hind coxa* (Fig. 44). Primitively, each hind coxa is smoothly rounded dorsally. 66.1—Each hind coxa bears a definite longitudinal carina along the dorsal surface, especially basally. 66.1.1—Each hind coxa bears a dorsal carina which is expanded and lamellate.

A simple hind coxa is considered primitive because this is the condition in most non-Aculeata (although the coxa is carinate in Trigonalidae) and in those aculeates judged to be the most primitive on the basis of other characters.

The development of a dorsal carina or tooth on the hind coxa has occurred on various occasions, sometimes rather equivocally. Such projections have also been lost again within some groups such as the mutillids (see section below for discussion) and brachycistidids (present in males of most species but absent in *Brachycistis*). This character is thus of little importance in establishing groupings. State 66.1 has developed on internodes 7-8, 12-14 and 21-22, in the thynnid, sierolomorphid and apterogynid groups, and in the males of the methochid and chyphotid groups. The expansion of the tooth into a lamella (66.1.1) is characteristic of the myrmosid group only, although it may

be approached within the brachycistidid group (*Colocistis* male).

67. *Hind tibial spur number*. Primitively, each hind tibia bears two spurs apically. 67.1—Each hind tibia bears a single spur apically.

A hind tibia with two spurs is considered primitive because this is the condition in most Hymenoptera, both non-aculeates and aculeates.

The loss of one of the hind tibial spurs has occurred on the tree only in the methochid group, thus not providing any information on higher relationships. A similar state is, however, found within the bethylid group (e.g., cleptid sp.) and a more extreme state, involving the loss of both spurs, has occurred within the apid (e.g., *Apis*) and formicid (e.g., *Crematogaster*) groups.

\*68. *Hind tibial calcar* (Fig. 43). Primitively, the hind tibial spurs are similar, showing no evidence of modification as calcaria. 68.1—The inner spur of the hind tibia is modified as a calcar by the formation of a basal dorsal tuft of bristles with little modification of the cuticular portion of the spur. 68.2—The inner spur of the hind tibia is modified as a calcar by a dorsal carinate expansion of the cuticle over a considerable length. 68.3—The inner spur of the hind tibia is modified as a calcar by pectinate elaboration of a dorsal carina. 68.4—The inner spur of the hind tibia is modified as a calcar by development of dorsal pectination but without carina formation.

Unmodified spurs are considered primitive because this is the condition in non-aculeates as well as in most Aculeata.

The formation of a calcar on the hind tibia has occurred at least four times but in different ways on each occasion. State 68.1 has developed on internode 16-17, thus associating the pompilid and rhopalosomatid groups quite strongly, as has been

noted by Riek (1970). States 68.2, 68.3 and 68.4 are characteristic of the vespid, formicid and methochid groups respectively (the last two are similar to the condition of the middle tibial spurs in these taxa). Different forms of hind tibial calcaria have also been developed within the sphecid (present in most but absent in a few such as *Astata*) and myzinid (e.g., *Myzinum* female) groups. Although some members of the apid group (e.g., *Halictus*) have the inner hind tibial spur with large teeth, this state does not appear to be comparable to calcar formation in the other groups.

\*69. *Modified mesosoma of apterous female* (Fig. 45). Primitively, the mesosoma of the female is essentially unmodified and similar to that of the male. 69.1—The female is apterous with the mesosoma modified so that there are movable sutures between the pro- and meso- and the meso- and metathorax, the mesonotal subdivisions are distinguishable, the prepectal sclerite is free and the mesepimeron is distinct. 69.1.1—The female has the mesosoma modified as in 69.1 except that the mesepimeron is not distinguishable externally. 69.1.1.1—The female has the mesosoma modified as in 69.1.1 except that the mesonotal subdivisions are not distinguishable and the prepectal sclerite is reduced although free. 69.2—The female is apterous with the mesosoma modified so that the pleura are flattened, there is a functional suture between the pro- and mesothorax, the metathoracic-propodeal suture is distinct but not functional dorsally, and the prepectal sclerite is fused to the mesepisternum. 69.2.1—The female has the mesosoma modified as in 69.2 except that the metathoracic-propodeal suture is obliterated dorsally. 69.2.2—The female has the mesosoma modified as in 69.2 except that the suture between the pronotum and mesothorax is non-functional but distinct, and the metathoracic-propodeal suture is

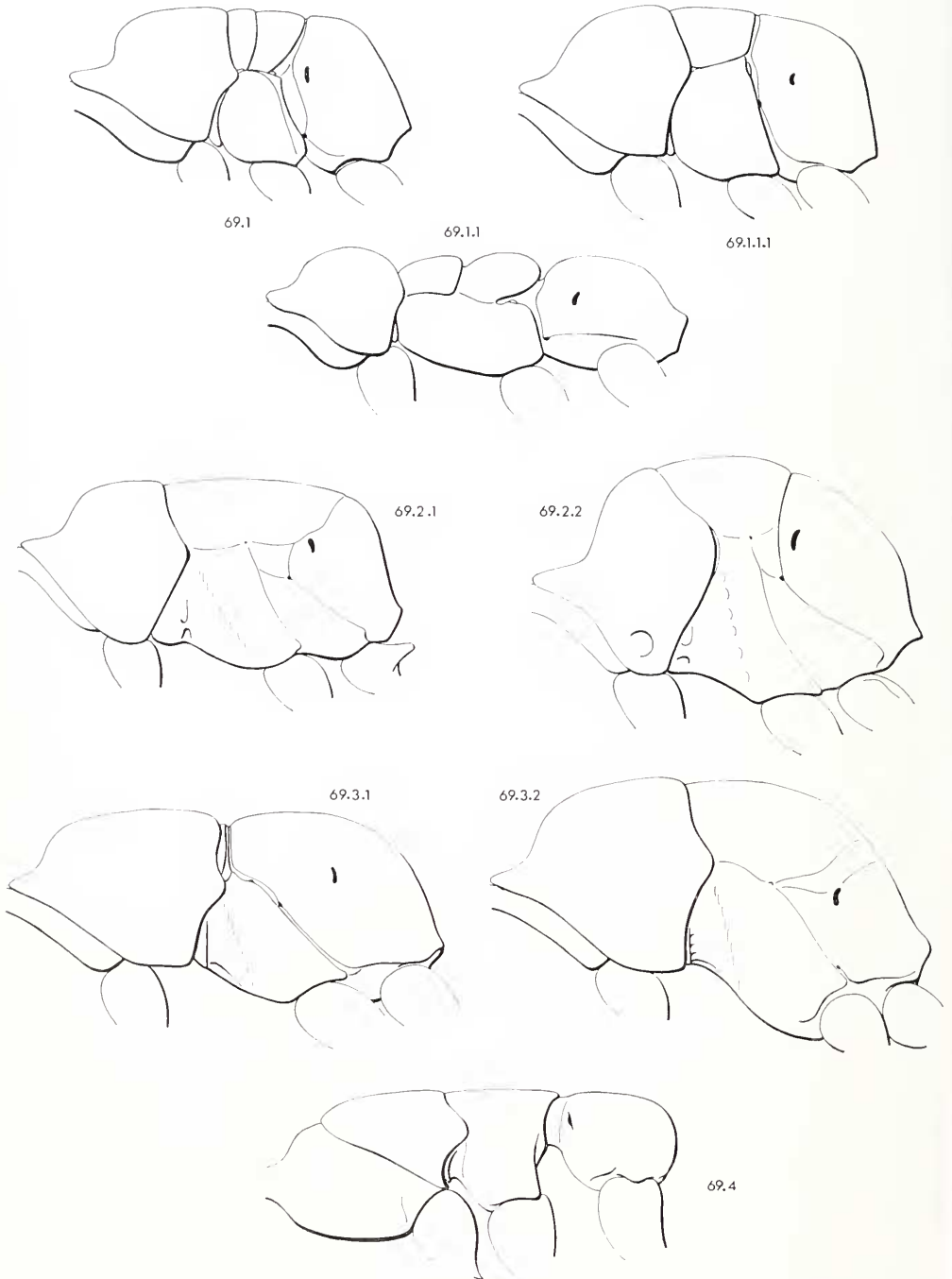


FIG. 45. Mesosoma, lateral view, showing derived states in apterous females (69.1 based on *Zaspilothynnus*; 69.1.1 on *Methocha*; 69.1.1.1 on *Bruesiella*; 69.2.1 on *Myrmosa*; 69.2.2 on *Pseudophotopsis*; 69.3.1 on *Typhoctoides*; 69.3.2 on *Apterogyna*; 69.4 on *Plumarius*).

indistinct dorsally. 69.3—The female is apterous with the mesosoma modified so that the pleura (especially the mesopleuron) are somewhat protuberant, the suture between the pronotum and the mesothorax is functional, the meso-metathoracic suture is visible but non-functional, the mesonotum is neither reduced nor enlarged, and the prepectal sclerite is fused to the mesepisternum. 69.3.1—The female has the mesosoma modified as in 69.3 except that the mesonotum is very short and transverse. 69.3.2—The female has the mesosoma modified as in 69.3 except that the meso-metathoracic suture is only indistinctly visible and the mesonotum is somewhat posteriorly produced. 69.4—The female is apterous with the mesosoma modified so that the pro-meso- and meso-metathoracic articulations are retained, the propleura are fused to form a rigid tube, and the meso- and metathoraces are separated by a deep lateral and ventral constriction, causing the metacoxal cavities to be considerably separated from the mesocoxal cavities.

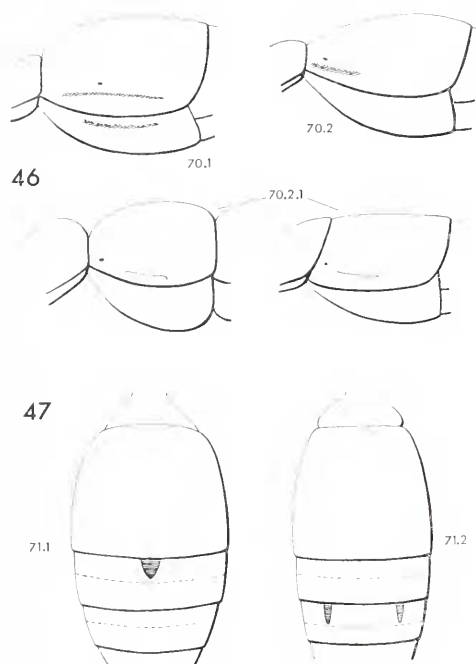
An unmodified mesosoma in the female is considered primitive because this is the condition in most Hymenoptera, both non-aculeates and aculeates.

Associated with aptery in the females (state 2.1), the mesosoma has been variously modified, as was shown by Reid (1941). (Although worker ants are primitively apterous and thus show mesosomal modifications, they are not included here because the queens are winged with no such mesosomal changes, except in a few highly specialized forms. The primitive condition in the formicids is thus not considered to involve this character.) There are at least four different basic patterns along which such modification has occurred, three of them linking various taxa into higher groupings. Because of the complexity and extent of the various modifications involved, each line of de-

velopment is considered to provide very good evidence of the relationships demonstrated.

The line based on 69.1 associates various members of the tiphoid complex. In this line it is apparent that each of the derived states is expressed only when accompanied by state 2.1, but that the potential for such expression exists even in the absence of winglessness in the female. Although state 69.1 is displayed in the thynnid group only, it has logically arisen on internode 10-11 since its derivatives are expressed in other taxa derived from that internode. State 69.1.1 is expressed in the entire methochid group and also in some members of the myzinid group (e.g., *Braunsomeria*), so that it must have arisen below node 13. In addition, its derivative state (69.1.1.1) is present in the brachycistidid group, so that state 69.1.1 is logically placed on internode 11-12. The line based on state 69.2 associates the myrmosid and mutillid groups. State 69.2 is logically derived on internode 8-9 and has apparently subsequently been modified in different directions in its two derivative groups, so that 69.2.1 appears in the myrmosids and 69.2.2 in the mutillids. The line based on 69.3 associates five taxa in the typhoctoid and bradynobaenoid lines, state 69.3 having been derived on internode 18-21. Its two derivative states are expressed in different lines; 69.3.1 appears on internode 21-22, strongly associating the typhoctid and eotillid groups, and 69.3.2 is placed on internode 21-23, strongly linking the chyphotid, apterogynid and bradynobaenid groups. State 69.4 has occurred in only the plumariid group. Apart from these states, aptery and various mesosomal modifications have occurred within certain other taxa, as is indicated in the discussion of character 2.

\*70. "*Felt lines*" (Fig. 46). Primitively, there are no modifications of the second metasomal segment in the form of differ-



FIGS. 46-47. Characters of Aculeata. 46, second metasomal segment, lateral view, showing derived states of "felt lines" (70.1 based on *Pseudophotopsis*, ♂; 70.2 on *Tynphoctes*, ♂; 70.2.1 on *Apterogyna*, ♀, and *Bradynobaenus*, ♀, left to right); 47, second to fourth metasomal segments, dorsal view, somewhat expanded, showing derived states of stridulitria (both composite).

entiated areas for the openings of subcuticular glandular organs. 70.1—There are longitudinally elongate and narrow depressed areas ("felt lines") on each side of the second metasomal segment on both tergum and sternum, each bearing dense short pubescence and the openings of secretory organs. 70.2—There is a longitudinally oval area ("felt line") developed on each side of the second metasomal segment on the tergum only, this bearing dense moderately long pubescence and the openings of secretory organs. 70.2.1—There is a longitudinal area on each side of the second metasomal tergum consisting of a line of cuticular depression or invagination but without dense pubescence.

A second metasomal segment without "felt lines" is considered primitive because

this is the condition in most Hymenoptera, both non-aculeates and aculeates.

Although it would at first seem likely that a structure as complex as a "felt line" would most probably have a single derivation, this is apparently not so. Despite the similarities between states 70.1 and 70.2, these do exhibit slight morphological differences, as was found by Debolt (1973). In addition, similar structures, in gross appearance at least, are present on the first metasomal tergum within the tiphiid group (*Paratiphia*) and ventrally on the pronotum within the mutillids (*Pseudophotopsis*). Some primitive members of the apid group (e.g., *Brachyhesma*, *Sericogaster*) bear a lateral "fovea" on the second metasomal tergum, which is apparently secretory although not as densely pubescent as in state 70.2; this is probably analogous (or even homologous) to a "felt line." Structures which are probably analogous are also found on the sixth metasomal sternum in some vespids (e.g., *Paravespula*; Spradbery, 1973).

State 70.1 is characteristic of the mutillid group only, within which it has undergone various modifications involving loss of the sternal or tergal elements or both. State 70.2 has occurred on internode 18-21 and links five taxa. Loss of the pubescence in the "felt line" resulting in a mere cuticular depression or invagination (70.2.1) has apparently taken place in the female on internode 23-24 so that male apterogynids have pubescent lines whereas the female has cuticular grooves. In the bradynobaenids the loss of pubescence has occurred in the male also and both sexes have lines along which the cuticle is apparently slightly invaginated. These structures have not previously been recorded in this group, and their presence is strong evidence of the relationship between the bradynobaenid, apterogynid and chyphotid groups and of these to the tynphoctids and cotillids.

\*71. *Stridulitra* (Fig. 47). Primitively, there are no specialized stridulatory organs on the metasoma. 71.1—There is a single stridulitrum developed as a small shield-shaped, finely transversely striated area mesally at the base of the third metasomal tergum. This rubs against a plectrum (ridge) on the underside of the posterior margin of the second tergum. 71.2—There is a pair of stridulitra developed as a fairly narrow, finely transversely striated, shield-shaped area on each side at the base of the fourth metasomal tergum. This rubs against a plectrum on the underside of the posterior margin of the third metasomal tergum on each side.

The absence of metasomal stridulitra is considered primitive because this is the condition in most Hymenoptera, both non-aculeates and Aculeata. The terminology is derived from that of Ashlock & Lattin (1963), although the "instrument" is moved against the plectrum in the Hymenoptera rather than the plectrum being the movable part. The fine structure of the mesal stridulitrum has been investigated by Hinton, Gibbs & Silberglid (1969).

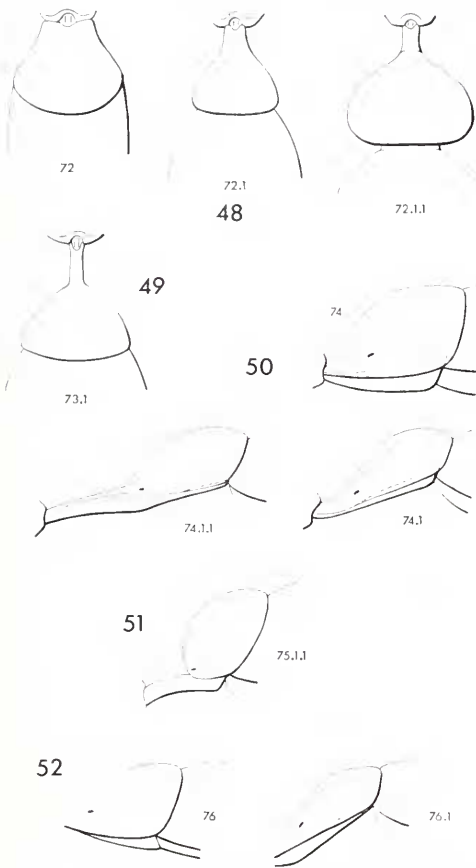
The development of a mesal stridulitrum (71.1) has occurred on internode 8-9 and thus strongly associates the myrmosid and mutillid groups. The strength of this state is, however, slightly reduced by the fact that a similar development has taken place within the formicid group (present in the poneroid and pseudomyrmecoid complexes but absent in the myrmecoid line; see Haskins & Ensmann, 1938; Markl, 1973) and within the rhopalosomatids (e.g., *Olixon*), where the form is somewhat different, however. Lateral stridulitra (71.2) are present in the typhoctid, cotillid and chyphotid groups and apparently arose on internode 18-21; they were subsequently lost on internode 23-24, being absent in the apterogynids and bradyobaenids. It seems more likely

that such a structure, apparently unique in the aculeates (although a very few members of the sphecoid group, e.g., *Pseudoplisus*, possess lateral stridulitra on the fourth and fifth terga) should have arisen once only, than that it had two independent origins resulting in identical expressions. Similar loss of stridulitra has apparently occurred in the *Ligyrocoris* group of Lygaeidae (Hemiptera) (Ashlock & Lattin, 1963), so that this possibility should not be rejected out of hand.

72. *Constriction of first metasomal tergum* (Fig. 48). Primitively, especially as viewed from above, the first metasomal tergum overlies the second and its surface contour merges smoothly with it in a continuous arc. 72.1—The posterior margin of the first metasomal tergum is slightly constricted so that there is a definite discontinuity between the contours of the first and second terga, but the first segment is not nodose. 72.1.1—The posterior margin of the first metasomal tergum is markedly constricted and differentiated from the second so that the first segment is definitely nodose.

An unconstricted first tergum is considered primitive because this is the condition in most Symphyta and many Terebrantia as well as in those Aculeata considered primitive on the basis of other characters.

Slight posterior constriction of the first metasomal tergum has apparently occurred on numerous occasions so that this state is of minimal use in establishing groups. State 72.1 has arisen on at least seven occasions, on internodes 8-9 and 11-12 in males only, 12-14 in females also, and 18-21 in both sexes, and in addition in the rhopalosomatid, formicid and scoliid groups. It is also present within various other taxa such as the sphecoids (e.g., *Trypargilum*), apids (e.g., *Osiris* female), sierolomorphids (e.g., *Sierolomorpha canadensis*) and vespids (e.g., *Monobia*).



FIGS. 48-52. Characters of Aculeata. 48, base of metasoma, dorsal view, showing primitive and derived states of constriction of first tergum (72 based on *Anthobosca*, ♂; 72.1 on *Typhoctes*, ♀, modified; 72.1.1 on *Apterogyna*, ♀); 49, base of metasoma, dorsal view, showing derived state of petiole (73.1 based on *Bradynobaenus*, ♀); 50, first metasomal segment, lateral view, showing primitive and derived states of lateral margin of tergum (74 based on *Sierolomorpha*, ♀; 74.1 on *Typhoctes*, ♀; 74.1.1 on *Chyphotes*, ♂); 51, first metasomal segment, lateral view, showing derived state of width of tergum (75.1.1 based on *Chyphotes*, ♀; Fig. 50, 74.1.1 represents 75.1 also); 52, base of metasoma, lateral view, showing primitive and derived states of differentiation of first sternum (76 based on *Anthobosca*, ♂; 76.1 on *Tiphia*, ♂, modified).

State 72.1.1 occurs only in the apterogynid group and also within the formicid group (all members except *Amblyoponini*; Wilson, Carpenter & Brown, 1967).

73. *Metasomal petiole* (Fig. 49). Primitively, the first metasomal segment is

evenly constricted anteriorly toward its articulation with the mesosoma. 73.1—The anterior extremity of the first metasomal segment is highly differentiated from the main body of the segment as a short petiole which is more or less cylindrical.

A non-petiolate first metasomal segment is considered primitive because this is the condition in the Symphyta and most other non-aculeates as well as in most Aculeata.

The formation of a definite petiole has occurred on internode 18-21 where a short, cylindrical petiole is characteristic of five taxa, and also in the formicid group. The strength of this character is, however, weakened by the fact that various petiolar modifications of the first metasomal segment have occurred within many other taxa such as the sphecids (e.g., *Ammophila*), myzinids (e.g., *Meria*, *Mesa*) and vespids (e.g., *Belonogaster*, *Eumenes*).

\*74. *Lateral margin of first metasomal tergum* (Fig. 50). Primitively, the first metasomal tergum broadly overlies the sternum laterally and is freely movable against it. 74.1—The first metasomal tergum overlies the sternum only posteriorly and narrowly, being closely associated with it but not fused except perhaps at the extreme base. 74.1.1—The first metasomal tergum overlies the sternum only posteriorly and narrowly and is fused to it along the petiole.

A first tergum that broadly overlies the sternum is considered to be primitive because this is the condition in most non-aculeates and in most members of the Aculeata.

The tendency toward fusion of the first tergum and sternum has apparently been established on internode 18-21 since state 74.1 associates the typhoctid and eotillid groups, and its derivative (74.1.1) has arisen on internode 21-23, linking the chyphotid, apterogynid and bradynobaenid



groups. This trend is almost unique and good evidence of these relationships although a rather similar condition is shown within the myzinid group (e.g., *Meria*). Different forms of fusion have occurred within other taxa such as the sphecid (e.g., *Chlorion*) and vespid (e.g., *Zethus*) groups.

\*75. *Width of first tergum* (Fig. 51). Primitively, the first metasomal tergum is broader than the sternum over its entire length due to its overlap of the sternum. 75.1—The first tergum is very narrow anteriorly, its lateral margin running along the dorsal surface of the petiole on each side. 75.1.1—The first tergum is completely absent anteriorly, the sternum apparently forming the petiole in its entirety.

A broad first tergum is considered primitive because this is the condition in most non-aculeates and in most members of the Aculeata.

Extreme reduction in width of the first tergum anteriorly (75.1) is characteristic only of the chyphotid, apterogynid and bradynobaenid groups and has occurred on internode 21-23. Complete absence of the tergum along the petiole (75.1.1) has apparently occurred only in the females of the chyphotid group, traces of the tergum being distinguishable to the base of the petiole in the males of that taxon. A state similar to 75.1 has, however, occurred within the myzinid group (e.g., *Meria*) and the absence of the tergum along the petiole has taken place within the sphecid group (e.g., *Prionyx*), although in a slightly different fashion from state 75.1.1. Despite these separate origins, this character provides quite good evidence of the relationship of the taxa subtended by internode 21-23.

76. *Differentiation of first sternum* (Fig. 52). Primitively, the first metasomal sternum overlies the second posteriorly and is not differentiated from it by any marked

discontinuities. 76.1—The first sternum is depressed and differentiated from the second by a deep constriction.

An undifferentiated first sternum is considered primitive because this is the condition in most non-aculeates and also in those members of the Aculeata considered to be primitive on the basis of other characters.

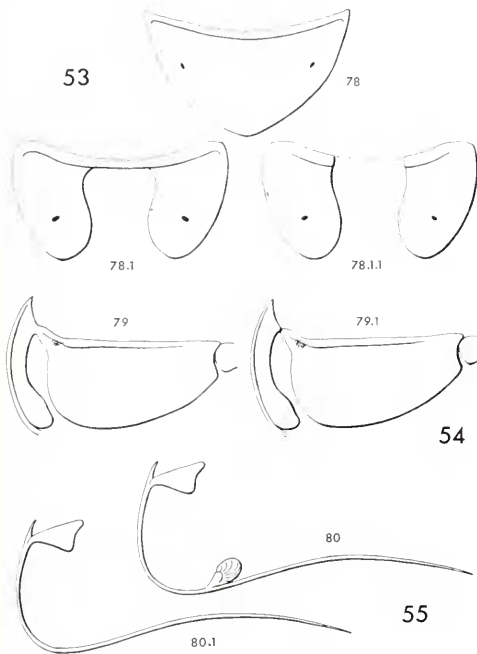
Posterior differentiation of the first sternum has apparently occurred at least three times, on internodes 8-9, 11-12 and 16-18 and also within the thynnid (e.g., *Diamma* female) and sphecid (e.g., *Cerceris*) groups at least, so that it is of little importance in establishing relationships, although there are differences in detail in the various occurrences.

77. *Constriction of second metasomal segment*. Primitively, the second metasomal segment is not at all constricted apically but its contours merge evenly with those of the third. 77.1—The second metasomal segment is strongly constricted apically, dorsally and ventrally as well as laterally, and is strongly differentiated from the third.

An unconstricted second metasomal segment is considered primitive because this is the condition in most Hymenoptera, both non-aculeates and aculeates.

A nodose second metasomal segment is characteristic only of the apterogynid group and is thus not of any importance in determining higher groupings. A similar state is also present within the formicid group (e.g., *Atta*).

\*78. *Seventh tergum of female* (Fig. 53). Primitively, the seventh metasomal tergum (eighth abdominal tergum) is somewhat exposed. It is evenly sclerotized over its entire length, forming a fairly long transverse sclerite. 78.1—The seventh metasomal tergum is retracted and entirely hidden. Its sclerotization is reduced to a short strip across the anterior margin con-



FIGS. 53-55. Characters of Aculeata. 53, seventh tergum of female, dorsal view, showing primitive and derived states (all composite); 54, gonocoxite IX of female, lateral view, showing primitive and derived states (both composite); 55, gonapophysis VIII of female, lateral view, showing primitive and derived states (both composite).

necting the lateral plates which bear the spiracles. 78.1.1—The seventh metasomal tergum is retracted and entirely hidden. Its sclerotization is entirely reduced mesally so that the lateral spiracular plates are linked by membrane only.

An exposed and fully sclerotized seventh tergum is considered primitive because this is the condition in the non-aculeate Hymenoptera.

Concealment and partial desclerotization of the seventh tergum in the female is characteristic of the entire group comprising the Aculeata (*sensu stricto*) as defined by Oeser (1961). Since this state (78.1; internode 1-4) has been attained only once in the entire Hymenoptera, it provides extremely good evidence of the holophyletic nature of this grouping. Although the seventh tergum is concealed

in the plumariids, this has occurred by enlargement of the sixth sternum which enfolds the seventh tergum, and not by anterior retraction of the seventh tergum under the sixth. State 78.1.1 is uniquely characteristic of the apid group and so does not serve to indicate any further higher groups.

\*79. *Gonocoxite IX of female* (Fig. 54). Primitively, section 1 of gonocoxite IX (Smith, 1970a) is dorsoventrally constricted but is not completely divided. 79.1—Section 1 of gonocoxite IX is dorsoventrally constricted and completely divided by an internal articulation.

The absence of an articulation within section 1 of the gonocoxite is considered primitive because this is the condition in all non-aculeate Hymenoptera as well as in most Aculeata.

The development of an articulation within section 1 of the gonocoxite is uniquely characteristic of the bethylid, scolebythid and plumariid groups (it even occurs in the highly modified genitalia of the Chrysididae; Oeser, 1961). This is thus a very strong character uniting these taxa into a holophyletic group, and has arisen on internode 1-2.

80. *Gonapophysis VIII of female* (Fig. 55). Primitively, each gonapophysis VIII bears a lamellate valve dorsally near the base. 80.1—Each gonapophysis VIII is simple and smooth dorsally with no trace of a valve.

A valve on the gonapophysis VIII is considered primitive because this is the condition in most Aculeata including those which are judged to be most primitive on the basis of other characters. A valve is also present in at least some non-aculeates (e.g., Ichneumonidae; Oeser, 1961).

The loss of the gonapophyseal valve has occurred on at least seven occasions, on internode 21-22 (in the typhoctids and

most likely the cotillid group (although the actual condition in the cotillids is unknown) and in the plumariid, sapygid, pompilid, vespid, chyphotid and bradynobaenid groups. Alternatively the valve could have been lost on internode 18-21 and then been redeveloped in the apterogynids. Although this would be more parsimonious placement on the cladogram, it seems intuitively less likely than multiple losses. In view of its large number of independent derivations, this state is not of any use in establishing higher groupings.

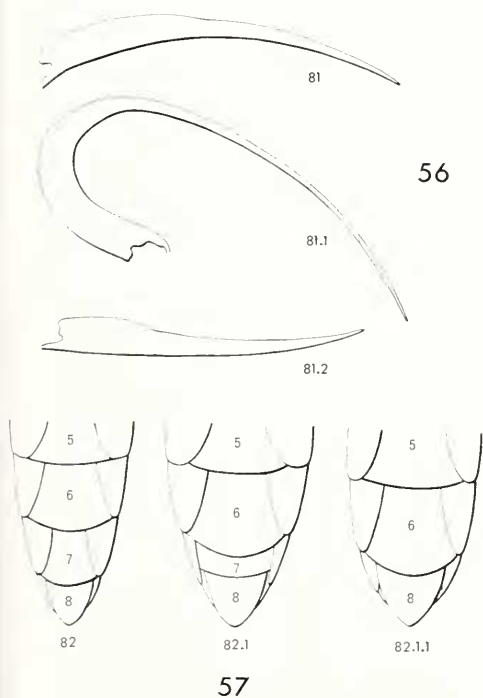
81. *Gonapophysis IX of female* (Fig. 56). Primitively, the gonapophysis IX (fused to its counterpart) is gently arcuate dorsally so that the apex is directed obliquely ventrally. 81.1—The gonapophysis IX is

strongly curved dorsally, especially basally, being somewhat elongated and with the apex directed downward. 81.2—The gonapophysis IX is almost straight or even slightly ventrally arcuate so that the apex is directed slightly upward or directly posteriorly.

A gently arcuate gonapophysis IX with the apex obliquely ventrally-directed is considered primitive because this is the condition in many Aculeata which are judged to be relatively primitive on the basis of other characters.

The degree and type of curvature of the gonapophysis IX is difficult to assign unequivocally to one of the designated states, and even when such decisions have been made, both derived states have apparently originated on numerous occasions. Nevertheless, the states do give some general indications of relationship and are somewhat useful. State 81.1 has apparently been derived on internodes 8-9 and 12-14 and in the methochid group. These taxa are all on the branch subtended by internode 6-7, the other members of which also show tendencies toward possession of this state, especially in elongation of the gonapophysis. State 81.1 is also present in the bradynobaenid group. State 81.2 has apparently been derived on internodes 4-5 and 18-21 (modified to 81.1 in the bradynobaenids) and in the rhopalosomatids and formicids. These are mostly groups on the branch subtended by internode 6-15, the other members of which also show a tendency toward a less elongate and less flexible gonapophysis.

82. *Seventh sternum of male* (Fig. 57). Primitively, the seventh metasomal sternum (eighth abdominal sternum) is well-developed, not much smaller than the sixth and clearly visible and exposed. 82.1—The seventh metasomal sternum is reduced and much smaller than the sixth although it is partly exposed. 82.1.1—The seventh metasomal sternum is greatly re-



FIGS. 56-57. Characters of Aculeata. 56, gonapophysis IX of female, showing primitive and derived states (all composite); 57, posterior region of metasoma of male, ventral view, showing primitive and derived states of seventh sternum, sterna numbered (all composite).

duced, much smaller than the sixth and completely hidden by it.

A well-developed seventh sternum is considered primitive because this is the condition in most Hymenoptera, both non-aculeates and aculeates.

Reduction of the seventh sternum has apparently occurred on numerous occasions. State 82.1 has arisen on internodes 6-7, 16-17 and 18-21, as well as in the plumariid and vespid groups. Furthermore, re-enlargement of the seventh sternum has apparently occurred on internode 12-13 and in the myrmosid group. State 82.1.1 has been derived on internode 12-14 and in the apid group. As in all characters involving relative sizes, it is difficult to assign the various states unequivocally, and it appears that because of multiple derivations this character cannot be used to provide reliable information on higher groupings.

\*83. *Form of male hypopygium* (Fig. 58). Primitively, the hypopygium (eighth metasomal or ninth abdominal sternum) is simple, unmodified and apically rounded although it may be reduced in size and concealed. 83.1—The hypopygium is much narrowed, forming a peglike structure, but is not acute apically. 83.2—The hypopygium bears three subequal spines apically, the spines about equal to the base in length (excluding the anterior process). 83.3—The hypopygium is modified to form a single upcurved spine or aculeus. 83.4—The hypopygium is apically produced as three spines, the middle one upcurved and much longer than the laterals which are considerably shorter than the base (excluding the anterior process). 83.4.1—The hypopygium is modified as in 83.4 except that the middle spine is only very slightly longer than the laterals and not upcurved.

A simple hypopygium is considered primitive because this is the condition in

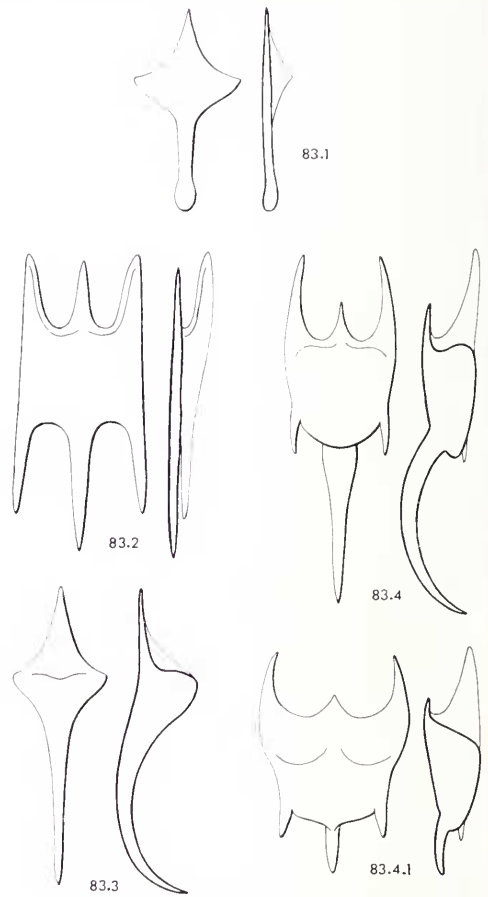


FIG. 58. Hypopygium of male, dorsal view and medial longitudinal section (approximate), showing derived states (83.1 based on *Sierolomorpha*; 83.2 on *Triclis*; 83.3 on *Paratiphia*; 83.4 on *Apterogyna*; 83.4.1 on *Bradynobaenus*).

most Hymenoptera, both non-Aculeata and Aculeata.

Each modification of the hypopygium has apparently only occurred once and where any one modification is present in more than one taxon it thus provides very good evidence of relationships. State 83.1 is characteristic of the sierolomorphids only and 83.2 of the scoliids. State 83.3 has been derived on internode 11-12 and associates four taxa in the tiphoid group, although this condition is approached within the thynnids (Salter, 1957). State 83.4 has originated on internode 21-23 and

links three taxa in the bradynobaenid group; the derived form of this state (83.4.1) is present in the bradynobaenid group only. States 83.2 and 83.4.1 are superficially similar but apparently have different origins and do appear somewhat different, especially when considered in conjunction with the following character (84). Within some of the other groups the hypopygium has often been modified in various ways but apparently never like any of the above states (except perhaps for 83.1).

84. *Concealment of male hypopygium.* Primitively, the hypopygium (eighth metasomal or ninth abdominal sternum) is not concealed by the preceding sterna. 84.1—The hypopygium is partially (up to the basal half) concealed by the preceding sterna. 84.2—The hypopygium is completely or almost completely concealed by the preceding sterna.

An unconcealed hypopygium is considered primitive because this is the condition in most Hymenoptera, both non-aculeates and aculeates.

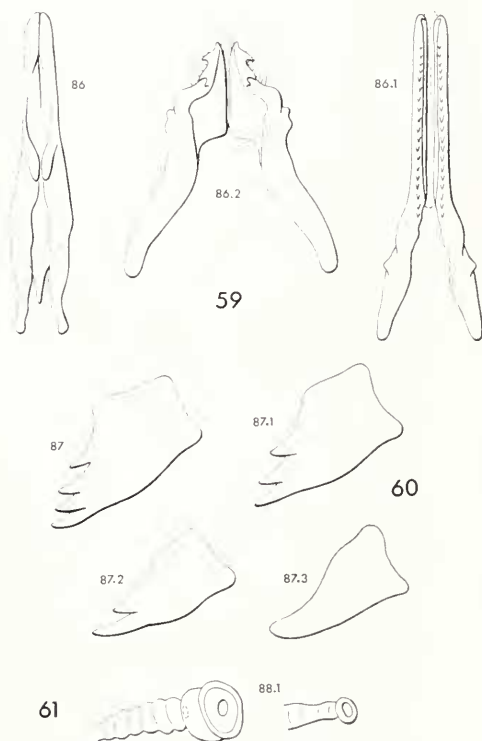
Partial or complete concealment of the hypopygium has apparently occurred on various occasions, mostly in single taxa, and is thus of minimal use in establishing relationships. State 84.1 has arisen in the anthoboscid and chyphotid groups and state 84.2 is present on internode 12-14 and in the apid, myrmosid, sierolomorphid and scoliid groups.

85. *Cercus of male.* Primitively, a cercus is present on each side of the composite tenth and eleventh abdominal tergum of the male. 85.1—The cercus is absent.

Presence of a cercus in the male is considered primitive because this is the condition in most Hymenoptera, both non-aculeate and aculeate, and also in insects in general. The cercus is absent in the female of all members of the Aculeata, however.

Loss of the cercus in the male has apparently occurred on at least four occasions and is thus not a strong character for indicating higher groups. State 85.1 has apparently arisen on internodes 12-14, 19-20 and 23-24 (in each case associating two taxa) and in the apid group.

\*86. *Gonapophysis IX of male* (Fig. 59). Primitively, the gonapophyses IX are fused dorsally to form a chitinous "notum" (Smith, 1970a) over much of their length. 86.1—The notal fusion between the gonapophyses is desclerotized so that the gonapophyses are linked by a membrane along their entire length dorsally. 86.2—The notal fusion between the gonapophyses is



FIGS. 59-61. Characters of Aculeata. 59, gonapophyses IX of male, ventral view, showing primitive and derived states (86 based on *Sierolomorpha*; 86.1 on *Trielis*; 86.2 on *Fedtschenkia*); 60, mandible of larva, showing primitive and derived states of teeth (all composite); 61, first and second spiracles of final instar larva, showing derived state (88.1 based on *Pseudomethoca*).

retracted basally and desclerotized so that the gonapophyses are linked only basally by a membrane, and are completely free apically, over much more than half their length.

Dorsally fused gonapophyses are considered to be primitive because this is the condition in most Hymenoptera, both non-Aculeata and Aculeata, as well as in insects in general (Smith, 1969, 1970a).

The particular modifications of the aedeagal notum have each apparently arisen only once in the taxa considered. State 86.1 is characteristic of the scoliid group only. State 86.2 has apparently arisen on internode 7-8 and associates the sapygid, myrmosid and mutillid groups strongly. The form in *Fedtschenkia* (sapygid) for example, is remarkably similar to that in *Pseudophotopsis* (mutillid), and the myrmosid type is easily derived by increased production of the dorsal area of the apex of each gonapophysis, a tendency which is present in the sapygids also. There are various other modifications involving desclerotization of the notum within other taxa such as the apids (Snodgrass, 1941), but generally not in detail like the described states.

87. *Larval mandibular teeth* (Fig. 60). Primitively, the final instar larva has strongly sclerotized mandibles which are quadridentate. 87.1—The final instar larva has tridentate mandibles. 87.2—The final instar larva has bidentate mandibles. 87.3—The final instar larva has simple unidentate mandibles.

Quadridentate mandibles are considered to be primitive because this is the condition in various aculeate taxa considered to be relatively primitive on the basis of other characters.

Although evaluation of the states of the larval mandibular teeth is considerably hampered by the complete absence of information on the larvae of the plumariid, scolebythid, brachycistidid, sierolomorphid,

typhoctid, eotillid, chyphotid, apterogynid and bradynobaenid groups, there nevertheless appear to be trends which may reflect the evolution of the mandible. Thus state 87.1 may have arisen on internode 15-16 (or possibly on internode 6-15 if it is present in the sierolomorphids). State 87.2 is present in the apids and sapygids but this may not be the primitive state for the latter group since the larvae of *Fedtschenkia* (the most generally primitive member) are unknown. State 87.3 is present in the rhopalosomatids, although it does occur within the apid group (e.g., *Apis*) and so is weakened, as well as not indicating higher groups.

\*88. *Larval spiracles* (Fig. 61). Primitively, the final instar larva has ten pairs of fully developed spiracles, all of similar size and complexity. 88.1—The final instar larva has only nine pairs of fully developed spiracles, the second thoracic spiracle being much reduced in size and complexity although still distinguishable.

Ten pairs of fully developed spiracles are considered primitive because this is the condition in most Hymenoptera, both non-aculeates and aculeates (Riek, 1970).

Reduction of the second thoracic spiracle in the final instar larva (88.1) has apparently occurred at least twice, on internode 6-7 and in the pompilid group. Unfortunately, as for character 87, information is lacking for nine taxa. The condition observed in the larva of *Sapyga* (Torchio, 1972) in which the spiracle is apparently not reduced (included on the tree as an apparent reversal to the primitive condition) may have resulted from the specialized cleptoparasitic habits of this genus; a more generalized member such as *Fedtschenkia* may have the spiracle reduced. Apart from this uncertainty, the usefulness of this character is also somewhat lessened by the fact that the second spiracle is reduced in early instar larvae of various other taxa like the

bethylids (e.g., *Chrysis*; Grandi, 1961). It is also apparently somewhat reduced in even the final instar larva of some vespids (e.g., *Dolichovespula*; Grandi, 1961). Nevertheless, because of various differences in detail, this character does seem to provide useful information on the relationship of the taxa above internode 6-7, as was suggested by Evans (1965), although his projection of the condition in the anthoboscid group has proved incorrect.

89. *Number of prey.* Primitively, each larva is supplied with a single host or prey individual and completes its development on this individual (V, P or M, and T appear once in the behavioral formula). 89.1—Each larva is supplied with numerous individuals of the host or prey and develops at the expense of many such individuals (V, P or M, and T appear repeatedly in the behavioral formula).

Use of a single prey individual for each larva is considered primitive because this is the situation in many Terebrantia and in various Aculeata considered relatively primitive on the basis of other characters.

The use of many prey individuals is apparently a trend shown in various taxa. Thus state 89.1 has arisen in the formicid and vespid groups and also in the apid group but in a somewhat different sense since the "prey" in the last instance is of vegetable and not animal origin. State 89.1 has also arisen within the sphecoid group (in many members but not in *Ampulex*, e.g.). Although an evaluation is greatly hampered by the lack of biological information on the plumariid, scolebythid, brachycistidid, sierolomorphid, typhoctid, cotillid, chyphotid, apterogynid and bradynobaenid groups, it appears that state 89.1 is of no use in delineating groups because of its multiple origins. It does, however, give some indication of relative advance on the tree.

90. *Nest construction.* Primitively, the prey is left exposed or in a natural cavity and no nest construction or excavation is undertaken by the female (T, I and C do not appear in the behavioral formula). 90.1—The prey is relocated by the female but no nest construction or excavation is undertaken (T appears in the behavioral formula but I and C do not). 90.1.1—The prey is relocated by the female which also constructs a specialized nest or excavation in which the prey is placed and which is closed after provisioning and oviposition (T, I and C appear in the behavioral formula). 90.1.2—The prey is relocated by the female which also constructs a specialized nest or excavation in which the prey is placed but which is not closed after oviposition since provisioning is continuous during the development of the young (T and I but not C appear in the behavioral formula). 90.1.3—The prey is relocated by the female which does not construct any specialized nest or excavation but which does close off the cavity in which the prey is placed (T and C but not I appear in the behavioral formula). 90.2—The prey is not relocated and no specialized nest construction or excavation is undertaken by the female which merely closes off the cavity in which the prey was discovered, after oviposition (C but not T and I appears in the behavioral formula).

Lack of any type of prey transportation or nest construction is considered primitive because this is the situation in many Terebrantia and in various Aculeata considered primitive on the basis of other characters.

As with character 89, it is difficult to determine the evolution of nest construction since data are lacking for nine of the taxa considered. Nevertheless, state 90.1 has apparently arisen at least twice, on internodes 4-5 (associating the sphecoid and apid groups) and 18-19 (linking the formicid, vespid and possibly the scoliid

groups). State 90.1.1 has arisen independently in the apid and vespidae groups; 90.1.2 is characteristic of the formicids; and 90.1.3 has arisen (apparently *de novo*, without prior origin of state 90.1) in the pompilid group. State 90.2 is characteristic of the myrmosid and mutillid groups and probably of the sapygids also, thus most likely having arisen on internode 7-8. This state is also present in the methochid group. Since behavior is by its very nature more plastic and thus probably more susceptible to evolutionary change than is morphology, thus aggravating problems of parallelism and convergence, this character appears to be of minimal significance in delineating groups, although it does provide some general indications of possible groupings.

91. *Oviposition sequence*. Primitively, oviposition occurs on the prey or host after it has been located [V (and usually P or M, and T) appears before O in the behavioral formula]. 91.1—Oviposition occurs in the empty nest chamber before the prey or host has been located (O appears before V, P or M, and T in the behavioral formula).

Oviposition after location of the host is considered primitive because this is the situation in the Terebrantia and in most Aculeata.

Early oviposition (91.1) has apparently arisen independently in the formicid and vespidae groups and is thus not of any significance in establishing relationships, although some connection may be implied by the fact that both occurrences have appeared on the branch subtended by internode 18-19.

92. *Type of provisions*. Primitively, the larvae are reared on food of animal origin, viz., other arthropods (subscripts "a" appear in the behavioral formula). 92.1—The larvae are reared on food of vegetable origin, usually pollen and nectar (sub-

scripts "v" appear in the behavioral formula).

Provisions of animal origin are considered primitive because these are the type used by most Terebrantia and by most Aculeata, including those considered relatively primitive on the basis of other characters.

The use of provisions of vegetable origin is characteristic of only the apid group, although a similar state has arisen within the vespidae group (most Masaridae but not *Euparagia*; Williams, 1927) and within the formicid group (the more advanced members; Wilson, 1971). This character is thus of no use in the derivation of higher groupings.

#### Character States Primitive for the Taxa Considered

The following accounts are composite and intended to apply to primitive members of the taxa concerned, i.e., the character states are those possessed by the ancestral members of the taxon. Such an ancestral form may be hypothetical since no particular extant member may show all the characters in the states given for a taxon. However, all the states listed are present in at least some modern species for each taxon. The accounts are thus usually not diagnostic in the usual sense for the taxa involved. Unless otherwise specified, each character state applies to both sexes of the adults, except for some characters of the mesosoma in taxa where the female is apterous, in which case the character states are those of the male. The numbers refer to the preceding discussion of the characters themselves.

The taxa are referred to below by informal names (the ending "-id" does not necessarily connote a group at the family level) so that the final classification derived from the cladogram may be more readily constructed from the taxa actually



considered, without the accounts of these taxa appearing under names which may differ from those adopted in the classification, or which may bear connotations at variance with those suggested by the final result. Nevertheless, the order in which the taxa are presented is as close to one reflecting evolutionary advance as possible, given the limitations of a linear arrangement. The taxa vary greatly in scope and categorical level, as may be judged from the listing of species examined for each, as well as the citation of which commonly recognized groups are included. Since it has proved impossible to check all previously identified specimens for accuracy of identification, the names used are those appearing on the determination labels associated with the specimens used, except for a few instances where changes in generic assignation have been made following recent revisions. Any misidentifications that may exist are actually of little or no significance for the derivation of the character states for the taxon concerned.

### 1. *Plumariid* group.

MATERIAL EXAMINED: *Myrmecopterina filicornis* ( $\delta$ ); *Plumarius* spp. ( $\delta$ , Argentina;  $\text{♀}$ , Peru); *Plumaroides andalgalensis* ( $\delta$ ). ("Plumariidae")

(Data also from Evans, 1967; Nagy, 1969a; Bradley, 1972. Nagy's "Heterogyninae"—*Heterogyna*—is also considered a member of this group.)

GENERAL—Sexual dimorphism considerable although male not more slender than female; male winged, female apterous (*Heterogyna* also; Nagy, *in litt.*) (1-2). No sterile caste (3). All pubescence simple (4).

HEAD—Clypeus of moderate size; antennae inserted low on face (5). Antennal socket simple, without tubercle (upper rim slightly produced in female) (6). Eye oval with inner margin shallowly sinuate (margin convex in female), not protuber-

ant; scattered short setae present (glabrous in female) (7-9). Three ocelli present (absent in female) (10). Genal secretory organ absent (11). Antenna with 13 segments in both sexes; axis of radicle not deviating much from that of scape (at an oblique angle in female); radicle not inserted into basal invagination of scape (12-14). Labio-maxillary complex not elongated; maxillary palpus 6-segmented (5-segmented in female); labial palpus 4-segmented (3-segmented in female) (15-17).

MESOSOMA—Pronotum large, not reduced mesally (reduced and short mesally in male), freely articulating with mesothorax; hind margin arcuate, almost straight (strongly concave in male); anterior "collar" very short (absent in female); posterolateral angle rounded, reaching tegula; posteroventral margin approximately straight; ventral angle rounded, not produced (18-23). Propleura mesally somewhat separated and shallowly diverging posteriorly (24). Prosternum somewhat sunken except anteriorly (25). Forecoxae somewhat separated (almost contiguous in female) (26). Mesonotum not anteriorly produced (enlarged, anteriorly produced in male); scutellum not much enlarged (27-28). Prepectus not fused to mesepisternum, discontinuous midventrally, the halves contiguous (29). Mesepimeron running the height of mesopleuron (30). Mesosternum essentially simple, without posterior projections (31). Mid-coxae slightly separated (almost contiguous in female) (32). Meso- and metapleura articulating (33). Metanotum not reduced medially; metapostnotum forming a distinct transverse area, fused to propodeum, slightly sunken but not invaginated (34-35). Endophragmal pit very close to anterior margin of metapleuron; no metapleural gland (36-37). Metasternum depressed anterolaterally to accommodate mid-coxae (entirely depressed in male),

well-differentiated from mesosternum, not anteriorly produced (38-40). Hind coxae slightly separated (41). Metathoracic-propodeal pleural suture visible dorsal to endophragmal pit, obliterated ventral to pit (42). Propodeum not shortened; disc and declivity not distinct but merging (43-44). Forewing with venation reduced apically; eight closed cells; veins 2s-m and 2m-cu absent (45-46). Pterostigma large and sclerotized (47-48). Hind wing with venation well-developed; three closed cells; veins A and J absent; cu-c originating proximal to point of separation of M and Cu; free section of Cu present (49-53). Basal hamuli dispersed along costa, not clustered (54). Plical lobe indicated by a moderate incision; jugal lobe absent (55-56). Legs slender, generally unmodified (femora and tibiae somewhat enlarged in female); arolia well-developed; claws toothed (simple in female) (57-59). Foretibia with single calcar almost straight, not highly modified (60). Mid-tibia with scattered weak spines (moderate spines in female); two simple spurs (61, 63-65). Hind coxa simple (66). Hind tibia with scattered weak spines; two simple spurs (62, 64, 67-68). Modified mesosoma of female with pronotum articulating with mesonotum; propleura fused ventrally and dorsally forming a rigid tube, slightly posteriorly produced in the midline ventrally; mesothorax with all sclerites fused, not distinguishable; metathorax much reduced, fused to propodeum; meso-metathoracic articulation very narrow and constricted; metacoxal cavities considerably separated from mesocoxal cavities so that mid-coxae are closer to forecoxae than hind coxae (69).

**METASOMA**—No specialized “felt lines” or stridulatory apparatus (70-71). First segment neither apically constricted nor petiolate (anteriorly narrowed and almost petiolate in female); first tergum with lateral margin overlying sternum, not fused to

it; first sternum not depressed, more or less continuous in contour with the second and overlying it (first sternum barely depressed and separated from second in female) (72-76). Second segment not apically constricted (77). Female with seventh tergum not mesally reduced (although enclosed by enlarged sixth sternum); articulation present within section 1 of gonocoxite IX; no valve on gonapophysis VIII; gonapophysis IX moderately curved with apex directed obliquely downward (78-81). Male with seventh sternum reduced but not entirely hidden; hypopygium simple, little modified although slightly narrowed; cercus present; gonapophyses IX with notal fusion well-developed, especially basally (82-86).

**LARVA**—UNKNOWN (that ascribed to *Plumarius* by Janvier, 1933:324, appears to be that of a mutillid from the figure and description).

**BEHAVIORAL FORMULA**—UNKNOWN.

## 2. *Bethylid* group.

**MATERIAL EXAMINED:** *Anisepyrus subviolaceus* (♂, ♀); *Apenesia columbana* (♂); *Bethylus amoenus* (♀); *Chrysis grandis* (♂, ♀); cleptid spp. (♂, California; ♀, India); *Deinodryinus henschawi* (♀); dryinid sp. (♀, Brazil); *Euchroeus purpuratus* (♂); *Goniozus foveolatus* (♀); *Goniozus* spp. (♂, New York; ♀, Florida); *Hedychridium carinulatum* (♂); *Omalus auratus* (♂); *Parasierola* spp. (♂, ♀, California); *Parnopes grandior* (♂); *Pristocera armifera* (♂); *Prosierola bicarinata* (♀); *Pseudisobrachium coxalis* (♂); *P. flavinervis* (♂); *Rhabdepyris megacephalus* (♂, ♀). (“Bethylidae,” “Chrysididae,” “Cleptidae,” “Dryinidae”) (Data also from Haupt, 1938; Grandi, 1961; Maa & Yoshimoto, 1961; Evans, 1964a. The following taxa are also considered to be members of this group: “Embolemlidae,” “Loboscelidiidae,” “Sclerogibbidae.”)

GENERAL—Sexual dimorphism minimal, both sexes of similar form and fully winged (1-2). No sterile caste (3). All pubescence simple (4).

HEAD—Clypeus of moderate size; antennae inserted low on face (5). Antennal socket simple, without tubercle (6). Eye oval with inner margin very shallowly sinuate, not protuberant; scattered pores without evident setae (7-9). Three ocelli present (10). Genal secretory organ absent (11). Antenna with 13 segments in both sexes; axis of radicle not deviating much from that of scape; radicle not set into basal invagination of scape (12-14). Labio-maxillary complex not elongated; maxillary palpus 6-segmented; labial palpus 3-segmented (15-17).

MESOSOMA—Pronotum large, not reduced mesally, freely articulating with mesothorax; hind margin arcuate, almost straight; anterior "collar" well-developed; posterolateral angle rounded, reaching tegula; posteroventral margin approximately straight; ventral angle rounded, not produced (18-23). Propleura mesally separated and diverging posteriorly (24). Prosternum not sunken (25). Forecoxae somewhat separated (26). Mesonotum not anteriorly produced; scutellum not enlarged (27-28). Prepectus not fused to mesepisternum, divided midventrally, the two halves contiguous (29). Mesepimeron running the height of mesopleuron (30). Mesosternum without posterior projections (31). Midcoxae somewhat separated (32). Meso- and metapleura articulating (33). Metanotum not reduced medially; metapostnotum indistinct, indistinguishable from propodeum medially, apparently not invaginated (34-35). Endophragmal pit very close to anterior margin of metapleuron; no metapleural gland (36-37). Metasternum depressed laterally to accommodate mid-coxae, well-differentiated from mesosternum, not anteriorly produced (38-40).

Hind coxae almost contiguous (41). Metathoracic-propodeal pleural suture barely visible dorsal to endophragmal pit, obliterated ventral to pit (42). Propodeum not shortened; disc and declivity slightly distinct but merging (43-44). Forewing with venation reduced apically; seven closed cells; vein M absent distal to separation from S; vein  $Cu_1$  absent distal to separation from  $Cu_2$ ; crossveins 1s-m, 2s-m and 2m-cu absent (45-46). Pterostigma large and sclerotized (47-48). Hind wing with venation reduced apically; one closed cell (C); vein M+Cu and all crossveins absent; veins A and J absent; traces of cu-e originating proximal to separation of M and Cu (49-52). Basal hamuli dispersed along costa, not clustered (54). Plical lobe indicated by a moderate incision; jugal lobe absent (55-56). Legs slender, unmodified; arolia well-developed; claws toothed (57-59). Foretibia with single calcar almost straight, not highly modified (60). Mid-tibia with some scattered setae spiniform; two simple spurs (61, 63-65). Hind coxa simple (66). Hind tibia with some scattered setae spiniform; two simple spurs (62, 64, 67-68).

METASOMA—No specialized "felt lines" or stridulatory apparatus (70-71). First segment neither apically constricted nor petiolate; first tergum with lateral margin overlying sternum, not fused to it; first sternum not depressed, more or less continuous in contour with the second (72-76). Second segment not apically constricted (77). Female with seventh tergum partially exposed, not much reduced; articulation present within section 1 of gonocoxite IX; valve present on gonapophysis VIII; gonapophysis IX moderately curved with apex directed obliquely downward (78-81). Male with seventh sternum not reduced nor hidden; hypopygium simple, unmodified; cercus present; gonapophyses IX with notal fusion well-developed (82-86).

FINAL INSTAR LARVA—Mandible quadridentate (87). Ten pairs of fully developed spiracles (88).

BEHAVIORAL FORMULA— $V_a P_a O$  (89-92).

### 3. *Scolebythid* group.

MATERIAL EXAMINED: *Clystopsenella longiventris* (♀). ("Scolebythidae")  
(Data also from Evans, 1963, 1967.)

GENERAL—Sexual dimorphism minimal, both sexes of similar form and fully winged (1-2). No sterile caste (3). All pubescence simple (4).

HEAD—Clypeus very short, reduced; antennae inserted very low on face (5). Antennal socket simple, with mesal margin only slightly raised, no tubercle (6). Eye oval with inner margin convex, not protuberant; scattered pores with short setae (7-9). Three ocelli present (10). Genal secretory organ absent (11). Antenna with 13 segments in both sexes; axis of radicle not deviating much from that of scape; radicle not inserted in basal invagination of scape (12-14). Labio-maxillary complex not elongated; maxillary palpus 6-segmented; labial palpus 4-segmented (15-17).

MESOSOMA—Pronotum large, not reduced mesally, freely articulating with mesothorax; hind margin arcuate, almost straight; anterior "collar" absent; posterolateral angle rounded, reaching tegula; posteroventral margin approximately straight; ventral angle rounded, not produced (18-23). Propleura mesally considerably separated and diverging posteriorly (24). Prosternum large, not sunken (25). Forecoxae broadly separated basally but posteriorly produced, thus becoming contiguous (26). Mesonotum not anteriorly produced; scutellum not enlarged (27-28). Prepectus not fused to mesepisternum, discontinuous midventrally, the halves considerably separated (29). Mesepimeron running the height of mesopleuron (30).

Mesosternum without posterior projection (31). Mid-coxae somewhat separated (32). Meso- and metapleura articulating (33). Metanotum reduced and very short medially; metapostnotum forming an indistinct transverse area, not clearly distinguishable from propodeum medially, not invaginated (34-35). Endophragmal pit very close to anterior margin of metapleuron; no metapleural gland (36-37). Metasternum depressed laterally to accommodate mid-coxae, well-differentiated from mesosternum, not anteriorly produced (38-40). Hind coxae contiguous (41). Metathoracic-propodeal pleural suture visible dorsal to endophragmal pit, obliterated ventral to pit (42). Propodeum not shortened; disc and declivity not distinct but merging (43-44). Forewing with venation reduced apically; six closed cells; vein M absent distal to separation from S; vein  $Cu_1 + Cu_2$  reduced distal to junction with  $1m-cu$ ; vein E absent distal to junction with  $cu-e$ ; crossveins  $1s-m$ ,  $2s-m$  and  $2m-cu$  absent (45-46). Pterostigma large and sclerotized (47-48). Hind wing with venation much reduced; no closed cells; veins A and J absent; origin of  $cu-e$  not determinable (49-52). Basal hamuli dispersed along costa, not clustered (54). Plical lobe indicated by a moderate incision; jugal lobe absent (55-56). Legs stout with femora inflated; arolia small but distinct; claws with blunt basal tooth (57-59). Foretibia with single calcar almost straight, not highly modified (60). Mid-tibia spineless; two simple spurs (61, 63-65). Hind coxa simple (66). Hind tibia spineless; two simple spurs (62, 64, 67-68).

METASOMA—No specialized "felt lines" or stridulatory apparatus (70-71). First segment neither apically constricted nor petiolate; first tergum with lateral margin overlying sternum, not fused to it; first sternum not depressed, more or less continuous in contour with the second and overlying it (72-76). Second segment not

apically constricted (77). Female with seventh tergum barely exposed, not mesally reduced; articulation present within section I of gonocoxite IX; valve present on gonapophysis VIII; gonapophysis IX moderately curved with apex directed obliquely downward (78-81). Male with hypopygium simple, unmodified (83) (additional character states of terminalia unknown).

LARVA—Unknown.

BEHAVIORAL FORMULA—Unknown.

#### 4. *Sphécid* group.

MATERIAL EXAMINED: ampulicid spp. (♂, Costa Rica; ♀, Sri Lanka); *Aphilanthops taurula* (♂, ♀); *Astata occidentalis* (♂, ♀); *Bembix hinei* (♂, ♀); *Cerceris bicornuta* (♂, ♀); *Chlorion aerarium* (♂, ♀); *Crabro largior* (♂, ♀); *Dasyproctus simillimus* (♂, ♀); *Epinysson bellus* (♂, ♀); *Gorytes provancheri* (♂, ♀); *Hapalomellinus albitomentosus* (♂, ♀); *Hoplisoides gulielmi* (♂, ♀); *Larropsis conferta* (♂, ♀); *Lyroda subita* (♂, ♀); *Mellinus* sp. (♂, ♀; Michigan); *Motes argentata* (♂, ♀); *Nysson aequalis* (♂, ♀); *Oxybelus cornutus* (♂, ♀); *Philanthus gibbosus* (♂, ♀); *Podalonia communis* (♂, ♀); *Prionyx foxi* (♂, ♀); *Pseneo montezuma* (♂, ♀); *Pseudoplisus phaleratus* (♂, ♀); *Sphex ichneumoneus* (♂, ♀); *Tachysphex tarsatus* (♂, ♀); *Trypargilum politum* (♂, ♀); *Zyzyx chilensis* (♂, ♀). ("Sphécidae" *sensu lato*) (Data also from Williams, 1919; Leclercq, 1954; Evans & Lin, 1956; Evans, 1959a, 1966.)

GENERAL—Sexual dimorphism minimal, male slightly smaller than female; both sexes fully winged (1-2). No sterile caste (3). All pubescence simple (4).

HEAD—Clypeus of moderate size; antennae inserted low on face (5). Antennal socket simple, without tubercle (6). Eye oval with inner margin shallowly sinuate,

not protuberant; scattered pores without evident setae (7-9). Three ocelli present (10). Genal secretory organ absent (11). Antenna with 13 segments in male, 12 segments in female; axis of radicle not deviating much from that of scape; radicle not set into basal invagination of scape (12-14). Labio-maxillary complex not elongated; maxillary palpus 6-segmented; labial palpus 4-segmented (15-17).

MESOSOMA—Pronotum reduced mesally, eliminating laterodorsal surface, fairly freely articulating with mesothorax, especially dorsally; hind margin broadly U-shaped; anterior "collar" well-developed; posterolateral angle much reduced above spiracular lobe, not reaching tegula; posteroventral margin slightly concave; ventral angle considerably produced mesally, almost meeting its counterpart midventrally (18-23). Propleura mesally slightly separated and shallowly diverging posteriorly (24). Prosternum sunken except for moderately large anterior rim (25). Forecoxae contiguous (26). Mesonotum somewhat anteriorly produced; scutellum not much enlarged (27-28). Prepectus depressed, fused to mesepisternum, continuous midventrally (29). Mesepimeron reduced, very short but distinguishable the entire height of mesopleuron (30). Mesosternum slightly posteriorly produced between coxal bases but not overlying them (31). Mid-coxae slightly separated (32). Meso- and metapleura not mutually movable but not completely fused (33). Metanotum not reduced medially; metapostnotum mesally greatly expanded posteriorly, forming most of apparent disc of propodeum, neither sunken nor invaginated (34-35). Metepimeron expanded ventrally anterior to endophragmal pit so that pit is some distance from anterior margin of metapleuron, additional ventral pit developed; no metapleural gland (36-37). Metasternum depressed laterally to accommodate mid-coxae, well-differentiated from

mesosternum except mesally, not anteriorly produced (38-40). Hind coxae contiguous (41). Metathoracic-propodeal pleural suture entirely visible, more distinct dorsal to endophragmal pit than ventrally (42). Propodeum effectively not shortened dorsally except as a result of development of metapostnotum; disc essentially absent but merging with declivity (43-44). Forewing with venation not much reduced apically; ten closed cells (45-46). Pterostigma fairly small and sclerotized (47-48). Hind wing with venation not much reduced apically; three closed cells; veins A and J present; cu-e originating proximal to separation of M and Cu; free section of Cu present (49-53). Basal hamuli dispersed along costa, not clustered (54). Plical lobe indicated by a moderate incision; large jugal lobe indicated by a shallow notch (55-56). Legs slender, generally unmodified; arolia well-developed; claws toothed (57-59). Foretibia with single calcar almost straight, not much modified (60). Mid-tibia with scattered moderate spines; two spurs, both slightly dorsally flattened with serrate margins (61, 63-65). Hind coxa simple (66). Hind tibia with scattered moderate spines; two spurs, both slightly dorsally flattened with serrate margins (62, 64, 67-68).

**METASOMA**—No specialized "felt lines" or stridulatory apparatus (70-71). First segment neither apically constricted nor petiolate; first tergum with lateral margin overlying sternum, not fused to it; first sternum not depressed, not differentiated from second but overlying it (72-76). Second segment not apically constricted (77). Female with seventh tergum hidden and reduced but with continuous anterior sclerotization; no articulation within section I of gonocoxite IX; valve present on gonapophysis VIII; gonapophysis IX almost straight with apex directed slightly upward (78-81). Male with seventh sternum neither reduced nor hidden; hypo-

pygium simple, unmodified; cercus present; gonapophyses IX with notal fusion well-developed (82-86).

**FINAL INSTAR LARVA**—Mandible quadridentate (87). Ten pairs of fully developed spiracles (88).

**BEHAVIORAL FORMULA**—V<sub>a</sub>P<sub>a</sub>T<sub>a</sub>O (89-92).

### 5. *Apid* group.

**MATERIAL EXAMINED:** *Andrena striatifrons* (♂, ♀); *Apis mellifera* (♂, ♀, ♀); *Aztecantidium xochipillium* (♂, ♀); *Brachyhesma incompleta* (♂, ♀); *Callomelitta* sp. (♂, ♀; Australia); *Colletes nudus* (♂, ♀); *Euglossa cordata* (♂, ♀); *Fidelia kobrowi* (♂); *Fidelia* sp. (♀, South Africa); *Halictus ligatus* (♂, ♀); *Hylaenus basalis* (♂, ♀); *Leioproctus herbstii* (♂, ♀); *Lithurgus apicalis* (♂, ♀); *Megachile parallela* (♂, ♀); *Megalopta centralis* (♂, ♀); *Melissodes microsticta* (♂, ♀); *Melitta tricincta* (♂, ♀); *Mesocheira bicolor* (♂, ♀); *Nomada superba* (♂, ♀); *Nomadopsis zebrata* (♂, ♀); *Nomia melanderi* (♂, ♀); *Osiris* spp. (♂, Brazil; ♀, Panama); *Protoxaea ferruginea* (♂, ♀); *Ptilothrix fructifer* (♂, ♀); *Sericogaster fasciata* (♂, ♀); *Systropha curvicornis* (♂, ♀); *Xylocopa micans* (♂, ♀). ("Colletidae," "Halictidae," "Oxaeidae," "Andrenidae," "Melittidae," "Fideliidae," "Megachilidae," "Anthophoridae," "Apididae")

(Data also from Snodgrass, 1941; Michener, 1944, 1953, 1965, 1974; Daly, 1964; Exley, 1968; Eickwort, 1969; Stephen, Bohart & Torchio, 1969.)

**GENERAL**—Sexual dimorphism minimal, male slightly smaller than female; both sexes fully winged (1-2). No sterile caste (3). Much erect pubescence plumose (4).

**HEAD**—Clypeus of moderate size; antennae inserted low on face (5). Antennal socket simple, without tubercle (6). Eye oval with inner margin shallowly sinuate, not protuberant; scattered pores without

evident setae (7-9). Three ocelli present (10). Genal secretory organ absent (11). Antenna with 13 segments in male, 12 segments in female; axis of radicle not deviating much from that of scape; radicle not set into basal invagination of scape (12-14). Labio-maxillary complex slightly elongated, especially in stipes and prementum; maxillary palpus 6-segmented; labial palpus 4-segmented (15-17).

**MESOSOMA**—Pronotum reduced mesally, eliminating laterodorsal surface, fairly freely articulating with mesothorax, especially dorsally; hind margin broadly U-shaped; anterior "collar" well-developed; posterolateral angle much reduced above spiracular lobe, reaching tegula; posteroventral margin slightly concave; ventral angle considerably produced mesally, almost meeting its counterpart midventrally (18-23). Propleura mesally slightly separated and shallowly diverging posteriorly (24). Prosternum sunken except for fairly long anterior region (25). Forecoxae contiguous (26). Mesonotum somewhat anteriorly produced; scutellum not greatly enlarged (27-28). Prepectus depressed, fused to mesepisternum, continuous midventrally (29). Mesepimeron much reduced, vaguely distinguishable only at dorsal extreme (30). Mesosternum very slightly posteriorly produced between coxal bases but not overlying them (31). Mid-coxae slightly separated (32). Meso- and metapleura not mutually movable but apparently not fused (33). Metanotum not reduced medially; metapostnotum mesally greatly expanded posteriorly, forming most of apparent disc of propodeum, neither sunken nor invaginated (34-35). Metepimeron ventrally expanded anterior to endophragmal pit so that pit is some distance from anterior margin of metapleuron, additional ventral pit developed; no metapleural gland (36-37). Metasternum depressed laterally to accommodate mid-coxae, mesally not well-differentiated from

mesosternum, not anteriorly produced (38-40). Hind coxae contiguous (41). Metathoracic-propodeal pleural suture visible dorsal to endophragmal pit, not distinguishable ventrally (42). Propodeum effectively not shortened dorsally except as a result of development of metapostnotum; disc essentially absent but merging with declivity (43-44). Forewing with venation somewhat reduced apically; ten closed cells (45-46). Pterostigma fairly small and sclerotized (47-48). Hind wing with venation only very slightly reduced apically; two closed cells; vein C reduced distally; vein A present, vein J absent; cu-e originating proximal to separation of M and Cu; free section of Cu present (49-53). Basal hamuli dispersed along margin, not clustered (54). Plical lobe indicated by a moderate incision; large jugal lobe indicated by a moderate incision (55-56). Legs slender, generally unmodified; arolia well-developed; claws toothed (57-59). Foretibia with single calcar almost straight, little modified (60). Mid-tibia with scattered weak spines; a single spur, slightly dorsally flattened with serrate margins (61, 63-65). Hind coxa simple (66). Hind tibia with scattered weak spines; two spurs, both slightly dorsally flattened with serrate margins (62, 64, 67-68).

**METASOMA**—No specialized "felt lines" or stridulatory apparatus (70-71). First segment neither apically constricted nor petiolate; first tergum with lateral margin overlying sternum, not fused to it; first sternum not depressed, not differentiated from second but overlying it (72-76). Second segment not apically constricted (77). Female with seventh tergum hidden, reduced, forming two separate sclerites; no articulation within section I of gonocoxite IX; valve present on gonapophysis VIII; gonapophysis IX almost straight with apex directed slightly upward (78-81). Male with seventh sternum reduced and concealed; hypopygium simple but con-

cealed; cercus absent; gonapophyses IX with notal fusion well-developed (82-86).

FINAL INSTAR LARVA—Mandible bidentate (87). Ten pairs of fully developed spiracles (88).

BEHAVIORAL FORMULA— $I(V_v T_v)^n MOC$  (89-92).

#### 6. *Anthoboscid* group.

MATERIAL EXAMINED: *Anthobosca erythro-nota* ( $\delta$ ,  $\varphi$ ); *A. ?flavicornis* ( $\delta$ ,  $\varphi$ ); *Anthobosca* spp. ( $\delta$ , South Africa;  $\varphi$ , Argentina); *Lalapa lusa* ( $\delta$ ,  $\varphi$ ). ("Anthoboscinae" of the "Tiphiidae")

(Data also derived from Turner, 1912; Janvier, 1933; Pate, 1947a; Evans, 1965.)

GENERAL—Sexual dimorphism moderate, male somewhat more slender than female; both sexes fully winged (1-2). No sterile caste (3). All pubescence simple (4).

HEAD—Clypeus of moderate size; antennae inserted low on face (5). Antennal socket simple, without tubercle (6). Eye oval with inner margin shallowly sinuate, not protuberant; scattered pores without evident setae (7-9). Three ocelli present (10). Genal secretory organ absent (11). Antenna with 13 segments in male, 12 segments in female; axis of radicle not deviating much from that of scape; radicle not set into basal invagination of scape (12-14). Labio-maxillary complex not elongated; maxillary palpus 6-segmented; labial palpus 4-segmented (15-17).

MESOSOMA—Pronotum large, not reduced mesally, freely articulating with mesothorax; hind margin shallowly arcuate; anterior "collar" well-developed; posterolateral angle rounded, reaching tegula; posteroventral margin approximately straight; ventral angle rounded, not produced (18-23). Propleura posteriorly contiguous mesally (24). Prosternum sunken except for relatively large anterior rim (25). Forecoxae very nearly contiguous (26). Mesonotum not anteriorly produced; scutellum

not enlarged (27-28). Prepectus not fused to mesepisternum, discontinuous midventrally, the halves considerably separated (29). Mesepimeron running the height of mesopleuron (30). Mesosternum with platelike projections posteromesally over coxal cavities (31). Mid-coxae slightly separated (32). Meso- and metapleura articulating (33). Metanotum not reduced medially; metapostnotum visible medially, somewhat invaginated (34-35). Endophragmal pit very close to anterior margin of metapleuron; no metapleural gland (36-37). Metasternum depressed anterolaterally to accommodate mid-coxae, slightly raised posteromesally, well-differentiated from mesosternum, not anteriorly produced (38-40). Hind coxae only slightly separated (41). Metathoracic-propodeal pleural suture entirely distinct (42). Propodeum not shortened; disc and declivity not distinct but merging (43-44). Forewing with venation not much reduced apically (slightly reduced in female); ten closed cells (45-46). Pterostigma fairly large and sclerotized (47-48). Hind wing with venation not reduced apically; three closed cells; veins A and J absent; cu originating distal to separation of M and Cu; free section of Cu present (49-53). Basal hamuli dispersed along margin, not clustered (54). Plical lobe indicated by a moderate incision; moderate jugal lobe present (55-56). Legs slender, generally unmodified (stouter in female with femora and tibiae enlarged); arolia well-developed; claws toothed (57-59). Foretibia with single calcar almost straight, not highly modified (60). Mid-tibia with scattered moderate spines; two simple spurs (spurs slightly dorsally flattened in female) (61, 63-65). Hind coxa simple (66). Hind tibia with scattered moderate spines; two simple spurs (spurs slightly dorsally flattened in female) (62, 64, 67-68).

METASOMA—No specialized "felt lines" or



stridulatory apparatus (70-71). First segment neither apically constricted nor petiolate; first tergum with lateral margin overlying sternum, not fused to it; first sternum not depressed, not highly differentiated from second (72-76). Second segment not apically constricted (77). Female with seventh tergum hidden, reduced but continuously sclerotized anteriorly; no articulation within section 1 of gonocoxite IX; valve present on gonapophysis VIII; gonapophysis IX moderately curved with apex directed obliquely downward (78-81). Male with seventh sternum somewhat reduced although not hidden; hypopygium slightly narrowed, lingulate, little modified, concealed basally; cercus present; gonapophyses IX with notal fusion well-developed, especially basally (82-86).

FINAL INSTAR LARVA—Mandible quadridentate (87). Nine pairs of fully developed spiracles, i.e., second pair reduced (88) (pers. obs.).

BEHAVIORAL FORMULA— $V_aP_aO$  (89-92).

### 7. *Thynnid* group.

MATERIAL EXAMINED: *Diamma bicolor* (♀); *Eirone* sp. (♂, Australia); *Elaphroptera scoliaeformis* (♂, ♀); *Elidothynnus basalis* (♂, ♀); *Hemithynnus apterus* (♂, ♀); thynnine spp. (♂, ♀; Argentina, Australia); *Thynnoides fumipennis* (♂, ♀); *Zaspilothynnus dilatatus* (♂, ♀). ("Thynninae" of the "Tiphidae")

(Data also from Turner, 1910; Janvier, 1933; Clausen, 1940; Reid, 1941; Pate, 1947a; Given, 1954, 1958, 1959; Salter, 1957; Ridsdill Smith, 1970a & b.)

GENERAL—Sexual dimorphism considerable although male only slightly more slender than female; male winged, female apterous (1-2). No sterile caste (3). All pubescence simple (4).

HEAD—Clypeus of moderate size, slightly dorsally produced; antennae inserted fairly low on face (5). Antennal socket simple

although slightly raised dorsomedially, without true tubercle (6). Eye oval with inner margin very shallowly sinuate, not protuberant; scattered pores without evident setae (7-9). Three ocelli present (10). Genal secretory organ absent (11). Antenna with 13 segments in male, 12 segments in female; axis of radicle not deviating much from that of scape; radicle not set into basal invagination of scape (12-14). Labio-maxillary complex not elongated; maxillary palpus 6-segmented; labial palpus 4-segmented (15-17).

MESOSOMA—Pronotum large, not reduced mesally, freely articulating with mesothorax; hind margin shallowly arcuate; anterior "collar" well-developed; posterolateral angle rounded, reaching tegula; posteroventral margin approximately straight; ventral angle rounded, not produced (18-23). Propleura posteriorly contiguous mesally (24). Prosternum sunken except for anterior rim (25). Forecoxae contiguous (26). Mesonotum not anteriorly produced; scutellum not enlarged (27-28). Prepectus not fused to mesepisternum, discontinuous midventrally, the halves considerably separated (29). Mesepimeron running the height of mesopleuron (30). Mesosternum with platelike projections posteromesally over coxal cavities (31). Mid-coxae slightly separated (32). Meso- and metapleura articulating (33). Metanotum not reduced medially; metapostnotum visible medially, somewhat invaginated (34-35). Endophragmal pit very close to anterior margin of metapleuron; no metapleural gland (36-37). Metasternum depressed anterolaterally to accommodate mid-coxae, slightly raised posteromesally, well-differentiated from mesosternum, not anteriorly produced (38-40). Hind coxae contiguous (41). Metathoracic propodeal pleural suture entirely distinct (42). Propodeum not shortened; disc and declivity not distinct but merging (43-44). Forewing with venation not

much reduced apically; ten closed cells (45-46). Pterostigma fairly large and sclerotized (47-48). Hind wing with venation not much reduced apically; three closed cells; veins A and J absent; cu-e originating distal to separation of M and Cu; free section of Cu present (49-53). Basal hamuli dispersed along costa, not clustered (54). Plical lobe barely indicated; moderate jugal lobe present (55-56). Legs slender, generally unmodified (somewhat stouter in female with femora and tibiae somewhat enlarged); arolia well-developed; claws toothed (57-59). Fore-tibia with single calcar almost straight, not highly modified (60). Mid-tibia with scattered moderate spines; two simple spurs (spurs slightly dorsally flattened in female) (61, 63-65). Hind coxa with weak dorsal carina (66). Hind tibia with scattered moderate spines; two simple spurs (spurs slightly dorsally flattened in female) (62, 64, 67-68). Modified mesosoma of female with pronotum large, articulating with mesothorax; mesonotum short; scuto-scutellar suture present; separate prepectal sclerite present; mesepimeron differentiated from mesepisternum; meso- and metapleura articulating; mesonotum very short and transverse; endophragmal pit very close to anterior margin of metapleuron; metathoracic-propodeal notal and pleural sutures visible (69).

**METASOMA**—No specialized "felt lines" or stridulatory apparatus (70-71). First segment neither apically constricted nor petiolate; first tergum with lateral margin overlying sternum, not fused to it; first sternum very slightly posteriorly depressed, not highly differentiated from second (72-76). Second segment not apically constricted (77). Female with seventh tergum hidden, reduced but continuously sclerotized anteriorly; no articulation within section I of gonocoxite IX; valve present on gonapophysis VIII; gonapophysis IX moderately curved with apex directed obliquely

downward (78-81). Male with seventh sternum somewhat reduced although not hidden; hypopygium simple, unmodified; cercus present; gonapophyses IX with notal fusion well-developed, especially basally (82-86).

**FINAL INSTAR LARVA**—Mandible quadridentate (87). Nine pairs of fully developed spiracles, i.e., second pair reduced (88) (pers. obs.).

**BEHAVIORAL FORMULA**— $V_a P_a O$  (89-92).

### 8. *Myzinid* group.

**MATERIAL EXAMINED:** *Braunsomeria mutilloides* (♀); *B. quadraticeps* (♂, ♀); *Meria infradentata* (♀); *M. perornata* (♂, ♀); *M. semirufa* (♂, ♀); *Mesa capitata* (♂, ♀); *Myzinum dubiosum* (♂, ♀); *M. quinquecinctum* (♂, ♀); *Pterombrus* spp. (♂, Mexico; ♀, Argentina). ("Myzininae" of the "Tiphidae") (Data also from Williams, 1928; Krombein, 1937, 1968; Clausen, 1940; Pate, 1947a; Evans, 1965.)

**GENERAL**—Sexual dimorphism marked, male much more slender than female; both sexes fully winged (1-2). No sterile caste (3). All pubescence simple (4).

**HEAD**—Clypeus of moderate size; antennae inserted fairly low on face (5). Antennal socket with dorsomesal rim somewhat raised by protuberance of frons, forming a frontal ledge (6). Eye oval with inner margin shallowly sinuate, not protuberant; scattered pores without evident setae (7-9). Three ocelli present (10). Genal secretory organ absent (11). Antenna with 13 segments in male, 12 segments in female; axis of radicle not deviating much from that of scape; radicle not set into basal invagination of scape (12-14). Labio-maxillary complex not elongated; maxillary palpi 6-segmented; labial palpi 4-segmented (15-17).

**MESOSOMA**—Pronotum large, not reduced mesally, freely articulating with mesotho-

rax; hind margin shallowly arcuate; anterior "collar" well-developed; posterolateral angle rounded, reaching tegula; posteroventral margin approximately straight; ventral angle rounded, not produced (18-23). Propleura posteriorly contiguous mesally (24). Prosternum sunken except for anterior rim (25). Forecoxae very nearly contiguous (26). Mesonotum not anteriorly produced; scutellum not enlarged (27-28). Prepectus not fused to mesepisternum, discontinuous midventrally, the halves considerably separated (29). Mesepimeron running the height of mesopleuron (30). Mesosternum with platelike projections posteromesally over coxal cavities (31). Mid-coxae slightly separated (32). Meso- and metapleura articulating (33). Metanotum not reduced medially; metapostnotum not visible medially, invaginated (34-35). Endophragmal pit very close to anterior margin of metapleuron; no metapleural gland (36-37). Metasternum depressed anterolaterally to accommodate mid-coxae, slightly raised posteromesally, well-differentiated from mesosternum, not anteriorly produced (38-40). Hind coxae slightly separated (41). Metathoracic-propodeal pleural suture entirely distinct (42). Propodeum not shortened; disc and declivity not distinct but merging (43-44). Forewing with venation not much reduced apically; ten closed cells (45-46). Pterostigma fairly large and sclerotized (47-48). Hind wing with venation not much reduced apically; three closed cells; veins A and J absent; cu-e originating distal to separation of M and Cu; free section of Cu present (49-53). Basal hamuli dispersed along margin, not clustered (54). Plical lobe indicated by a moderate incision; long jugal lobe marked by a deep incision (55-56). Legs slender, generally unmodified (stouter in female with femora and tibiae enlarged); arolia well-developed; claws toothed (57-59). Foretibia with single calcar almost

straight, not highly modified (60). Mid-tibia with scattered moderate spines; two simple spurs (spurs slightly dorsally flattened in female) (61, 63-65). Hind coxa simple (66). Hind tibia with scattered moderate spines; two simple spurs (spurs slightly flattened in female) (62, 64, 67-68).

**METASOMA**—No specialized "felt lines" or stridulatory apparatus (70-71). First segment neither apically constricted nor petiolate (slightly constricted in male); first tergum with lateral margin overlying sternum, not fused to it; first sternum extensively depressed, most strongly so posteriorly, separated from second by a deep constriction (72-76). Second segment not apically constricted (77). Female with seventh tergum hidden, reduced but continuously sclerotized anteriorly; no articulation within section 1 of gonocoxite IX; valve present on gonapophysis VIII; gonapophysis IX moderately curved with apex directed obliquely downward (78-81). Male with seventh sternum neither reduced nor hidden; hypopygium a single upcurved spine, hardly concealed basally; cercus present; gonapophyses IX with notal fusion extensive (82-86).

**FINAL INSTAR LARVA**—Mandible quadridentate (87). Nine pairs of fully developed spiracles, i.e., second pair reduced (88).

**BEHAVIORAL FORMULA**—V<sub>a</sub>P<sub>a</sub>O (89-92).

### 9. *Methochid* group.

**MATERIAL EXAMINED:** *Methocha haemarrhoidalis* (♀); *M. minima* (♀); *M. mosotuana* (♂, ♀); *M. stygia* (♂, ♀). ("Methochinae" of the "Tiphidae") (Data also from Williams, 1919; Pate, 1947a; Burdick & Wasbauer, 1959; Hamann, 1960; Evans, 1965; Wilson & Farish, 1973.)

**GENERAL**—Sexual dimorphism considerable, male much more slender than female; male winged, female apterous (1-2). No

sterile caste (3). All pubescence simple (4).

**HEAD**—Clypeus of moderate size; antennae inserted fairly low on face (5). Antennal socket with dorsomesal rim only very slightly raised, forming a very slight frontal ledge (6). Eye oval with inner margin obliquely convex, not protuberant; many scattered pores with moderately long setae (7-9). Three ocelli present (10). Genal secretory organ absent (11). Antenna with 13 segments in male, 12 segments in female; axis of radicle not deviating much from that of scape; radicle not set into basal invagination of scape (12-14). Labio-maxillary complex not elongated; maxillary palpus 6-segmented; labial palpus 4-segmented (15-17).

**MESOSOMA**—Pronotum large, not reduced mesally, freely articulating with mesothorax; hind margin shallowly arcuate; anterior "collar" well-developed; posterolateral angle rounded, reaching tegula; posteroventral margin slightly concave; ventral angle rounded, not produced (18-23). Propleura posteriorly contiguous mesally (24). Prosternum sunken except for anterior rim (25). Forecoxae contiguous (26). Mesonotum not anteriorly produced; scutellum not enlarged (27-28). Prepectus not fused to mesepisternum, discontinuous midventrally, the halves considerably separated (29). Mesepimeron running the height of mesopleuron (30). Mesosternum essentially simple but with dentate projections anteromesal to coxal cavities (31). Mid-coxae slightly separated (32). Meso- and metapleura articulating (33). Metanotum not reduced medially; metapostnotum barely visible medially, invaginated (34-35). Endophragmal pit very close to anterior margin of metapleuron; no metapleural gland (36-37). Metasternum depressed anterolaterally to accommodate mid-coxae, slightly raised posteromesally, well-differentiated from mesosternum, not anteriorly produced (38-40). Hind coxae

contiguous (41). Metathoracic-propodeal pleural suture visible dorsal to endophragmal pit, not distinguishable ventrally (42). Propodeum not shortened; disc and declivity not distinct but merging (43-44). Forewing with venation not much reduced apically; nine closed cells; vein S incomplete just proximal to junction with r-s (45-46). Pterostigma fairly large and sclerotized (47-48). Hind wing with venation only slightly reduced apically; two closed cells; vein C reduced distally; veins A and J absent; cu-e originating distal to separation of M and Cu; free section of Cu present (49-53). Basal hamuli dispersed along margin, not clustered (54). Plical lobe indicated by a moderate incision; moderate jugal lobe present (55-56). Legs slender, generally unmodified; arolia well-developed; claws toothed (57-59). Foretibia with single calcar almost straight, not highly modified (60). Midtibia with scattered weak spines; two simple spurs (only one, modified as calcar by dorsal pectination in female) (61, 63-65). Hind coxa simple (with well-developed dorsal carina in male) (66). Hind tibia with scattered weak spines; two spurs, the inner modified as calcar by dorsal pectination (only one spur, similarly modified, in female) (62, 64, 67-68). Modified mesosoma of female much narrowed; pronotum large, articulating with mesothorax; separate prepectal sclerite present; mesothorax long dorsally; scuto-scutellar suture present; mesepimeron not differentiated from mesepisternum; meso- and metapleura freely articulating; metathorax with notum very short and transverse; metapleuron reduced anterior to endophragmal pit; metathoracic-propodeal notal and pleural sutures visible dorsal to pit, not discernible ventrally; metacoxal cavities somewhat separated from mesocoxal cavities although mid-coxae still closer to hind coxae than to forecoxae (69).

**METASOMA**—No specialized "felt lines" or

stridulatory apparatus (70-71). First segment neither apically constricted nor petiolate (slightly constricted in male); first tergum with lateral margin overlying sternum, not fused to it; first sternum depressed, especially posteriorly, separated from second by a deep constriction (72-76). Second segment not apically constricted (77). Female with seventh tergum hidden, reduced but continuously sclerotized anteriorly; no articulation within section I of gonocoxite IX; valve present on gonapophysis VIII; gonapophysis IX considerably curved, especially basally, with apex directed downward (78-81). Male with seventh sternum not reduced nor hidden; hypopygium a single up-curved spine not concealed basally; cercus present; gonapophyses IX with notal fusion extensive (82-86).

FINAL INSTAR LARVA—Mandible quadridentate (87). Nine pairs of fully developed spiracles, i.e., second pair reduced (88).

BEHAVIORAL FORMULA— $V_a P_a OC$  (89-92).

#### 10. *Tiphid* group.

MATERIAL EXAMINED: *Krombeinia nayarita* ( $\delta$ ,  $\varphi$ ); *Neotiphia rostrata* ( $\delta$ ,  $\varphi$ ); *Paratiphia aequalis* ( $\delta$ ,  $\varphi$ ); *P. neomexicana* ( $\delta$ ,  $\varphi$ ); *Tiphia letalis* ( $\delta$ ,  $\varphi$ ); *T. popillivora* ( $\delta$ ,  $\varphi$ ). ("Tiphinae" of the "Tiphidae")

(Data also from Allen & Jaynes, 1930; Clausen & Gardner, 1932; Pate, 1947a; Allen & Krombein, 1964; Evans, 1965; Nagy, 1967; Allen, 1972.)

GENERAL—Sexual dimorphism slight, male only a little more slender than female; both sexes fully winged (1-2). No sterile caste (3). All pubescence simple (4).

HEAD—Clypeus of moderate size; antennae inserted low on face (5). Antennal socket simple, without tubercle (6). Eye oval with inner margin shallowly sinuate, not protuberant; scattered pores without evident setae (7-9). Three ocelli present

(10). Genal secretory organ absent (11). Antenna with 13 segments in male, 12 segments in female; axis of radicle not deviating much from that of scape; radicle not set into basal invagination of scape (12-14). Labio-maxillary complex not elongated; maxillary palpus 6-segmented; labial palpus 4-segmented (15-17).

MESOSOMA—Pronotum large, not reduced mesally, freely articulating with mesothorax; hind margin shallowly arcuate; anterior "collar" well-developed; posterolateral angle very slightly dorsally produced anterior to tegula, thus appearing truncate but reaching tegula; posteroventral margin somewhat concave; ventral angle more or less acute but not produced (18-23). Propleura posteriorly contiguous mesally (24). Prosternum sunken except for anterior rim (25). Forecoxae contiguous (26). Mesonotum not anteriorly produced; scutellum not enlarged (27-28). Prepectus not fused to mesepisternum, discontinuous midventrally, the halves considerably separated (29). Mesepimeron running the height of mesopleuron (30). Mesosternum with platelike projections posteromesally over coxal cavities (31). Mid-coxae somewhat separated (32). Meso- and metapleura not mutually movable although not fused (33). Metanotum not reduced medially; metapostnotum not visible medially, invaginated (34-35). Metepisternum somewhat expanded anterior to endophragmal pit so that pit is some distance from anterior margin of metapleuron but pleural sulcus is very indistinct; no metapleural gland (36-37). Metasternum depressed anterolaterally to accommodate mid-coxae, raised posteromesally, well-differentiated from mesosternum, not anteriorly produced (38-40). Hind coxae slightly separated (41). Metathoracic-propodeal pleural suture not distinguishable (42). Propodeum not shortened; disc and declivity distinctly separated by a transverse carina (43-44). Forewing with venation

reduced apically; nine closed cells; vein S incomplete just distal to separation from M (45-46). Pterostigma fairly large and sclerotized (47-48). Hind wing with venation reduced apically; three closed cells; veins A and J absent; cu-e originating distal to separation of M and Cu; free section of Cu present although reduced to a spur (49-53). Basal hamuli dispersed along margin, not clustered (54). Plical lobe marked by a moderate incision; long jugal lobe marked by an incision (55-56). Legs fairly slender, little modified (stouter in female with femora and tibiae enlarged); arolia well-developed; claws toothed (57-59). Foretibia with single calcar almost straight, not highly modified (60). Mid-tibia with scattered moderate spines; two simple spurs (spurs slightly dorsally flattened in female) (61, 63-65). Hind coxa with weak dorsal carina basally (66). Hind tibia with scattered moderate spines; two simple spurs (spurs slightly dorsally flattened in female) (62, 64, 67-68).

**METASOMA**—No specialized "felt lines" or stridulatory apparatus (70-71). First segment slightly constricted apically, not petiolate; first tergum with lateral margin overlying sternum, not fused to it; first sternum posteriorly depressed, separated from second by a deep constriction (72-76). Second segment not apically constricted (77). Female with seventh tergum hidden, reduced but continuously sclerotized anteriorly; no articulation within section I of gonocoxite IX; valve present on gonapophysis VIII; gonapophysis IX considerably curved, especially basally, with apex directed downward (78-81). Male with seventh sternum reduced and hidden; hypopygium a single up-curved spine, almost entirely concealed; cercus absent; gonapophyses IX with notal fusion extensive (82-86).

**FINAL INSTAR LARVA**—Mandible quadridentate (87). Nine pairs of fully developed spiracles, i.e., second pair reduced (88).

**BEHAVIORAL FORMULA**— $V_aP_aO$  (89-92).

### 11. *Brachycistidid* group.

**MATERIAL EXAMINED:** *Acanthetropis* spp. ( $\delta$ ; Arizona, New Mexico); *Aglyptacros sulcatus* ( $\eta$ ); *Brachycistis alcanor* ( $\delta$ ); *B. alutacea* ( $\eta$ ); *B. emarginata* ( $\eta$ ); *B. inaequalis* ( $\delta$ ); *Bruesiella* sp. ( $\eta$ , Arizona); *Colocistis* spp. ( $\delta$ ; Arizona, New Mexico); *Quemaya perpunctata* ( $\delta$ ). ("Brachycistidinae" of the "Tiphidae")

(Data also from Mickel & Krombein, 1942; Pate, 1947a; Wasbauer, 1966, 1968; Krombein, 1967.)

**GENERAL**—Sexual dimorphism considerable although male not more slender than female; male winged, female apterous (1-2). No sterile caste (3). All pubescence simple (4).

**HEAD**—Clypeus of moderate size (very short in female); antennae inserted fairly low on face (5). Antennal socket simple, without tubercle (6). Eye broadly oval, almost round, with inner margin shallowly sinuate, somewhat protuberant, scattered pores with short setae (eye reduced, oval with inner margin convex, flattened, glabrous, without pores in female) (7-9). Three ocelli present (absent in female) (10). Genal secretory organ absent (11). Antenna with 13 segments in male, 12 segments in female; axis of radicle not deviating much from that of scape; radicle not set into basal invagination of scape (12-14). Labio-maxillary complex not elongated; maxillary palpus 6-segmented; labial palpus 4-segmented (15-17).

**MESOSOMA**—Pronotum large, not reduced mesally, freely articulating with mesothorax; hind margin shallowly arcuate (deeply arcuate in male); anterior "collar" well-developed; posterolateral angle very slightly dorsally produced anterior to tegula thus appearing truncate but reaching tegula; posteroventral margin some-

what concave; ventral angle rounded, almost acute but not produced (18-23). Propleura posteriorly contiguous mesally (24). Prosternum sunken except for anterior rim (25). Forecoxae very nearly contiguous (26). Mesonotum somewhat anteriorly produced; scutellum not enlarged (27-28). Prepectus not fused to mesepisternum, discontinuous midventrally, the halves considerably separated and much reduced in length (29). Mesepimeron running the height of mesopleuron (30). Mesosternum with platelike projections posteromesally over coxal cavities (31). Mid-coxae somewhat separated (32). Meso- and metapleura not mutually movable although not fused (33). Metanotum not reduced medially; metapostnotum barely visible medially, invaginated (34-35). Metepisternum somewhat expanded anterior to endophragmal pit so that pit is some distance from anterior margin of metapleuron but pleural sulcus is very indistinct; no metapleural gland (36-37). Metasternum depressed anterolaterally to accommodate mid-coxae, slightly raised posteromesally, well-differentiated from mesosternum, not anteriorly produced (38-40). Hind coxae contiguous (41). Metathoracic-propodeal pleural suture visible dorsal to endophragmal pit, barely discernible ventrally (42). Propodeum not shortened; disc and declivity fairly distinct (43-44). Forewing with venation reduced apically; ten closed cells (45-46). Pterostigma large and sclerotized (47-48). Hind wing with venation reduced apically; three closed cells; veins A and J absent; cu-e originating distal to separation of M and Cu; free section of Cu present although reduced to a spur (49-53). Basal hamuli absent (54). Plical lobe indicated by a shallow incision; moderate jugal lobe present (55-56). Legs slender, generally unmodified (stouter in female with femora and tibiae enlarged); arolia well-developed; claws simple (57-

59). Foretibia with single calcar almost straight, not highly modified (58). Midtibia with scattered moderate spines; a single simple spur (spur slightly dorsally flattened in female) (61, 63-65). Hind coxa with weak dorsal carina basally (66). Hind tibia with scattered moderate spines; two simple spurs (spurs slightly dorsally flattened in female) (62, 64, 67-68). Modified mesosoma of female with pronotum large, articulating with mesothorax, its hind margin almost straight; mesonotum short; scuto-scutellar suture obliterated; separate prepectal sclerite present although much reduced; mesepimeron not differentiated from mesepisternum externally; meso- and metapleura articulating; metanotum extremely short and transverse, fused to propodeum, essentially not discernible; metapleuron greatly shortened anterior and dorsal to endophragmal pit; metathoracic-propodeal notal and pleural sutures discernible dorsal to pit, completely obliterated ventrally (69).

**METASOMA**—No specialized "felt lines" or stridulatory apparatus (70-71). First segment slightly constricted apically (more so in male), not petiolate; first tergum with lateral margin overlying sternum, not fused to it; first sternum entirely depressed, separated from second by a deep constriction (72-76). Second segment not apically constricted (77). Female with seventh tergum hidden, reduced but completely sclerotized anteriorly; no articulation within section I of gonocoxite IX; valve present on gonapophysis VIII; gonapophysis IX considerably curved, especially basally, with apex directed downward (78-81). Male with seventh sternum reduced and hidden; hypopygium a single upcurved spine, mostly concealed; cercus absent; gonapophyses IX with notal fusion extensive (82-86).

**LARVA**—Unknown.

**BEHAVIORAL FORMULA**—Unknown.

12. *Sapygid* group.

MATERIAL EXAMINED: *Fedtschenkia anthracina* (♂, ♀); *Polochrum repandum* (♂); *Sapyga clavicornis* (♀); *S. martinii* (♀); *Sapyga* sp. (♀, Colorado). ("Sapygidae") (Data also from Pate, 1947c; Bradley, 1955; Oeser, 1961; Guiglia, 1963, 1969; Tobias, 1965; Bohart & Schuster, 1972; Torchio, 1972.)

GENERAL—Sexual dimorphism minimal, both sexes of similar form and fully winged (1-2). No sterile caste (3). All pubescence simple (4).

HEAD—Clypeus of moderate size; antennae inserted fairly low on face (5). Antennal socket with dorsomesal rim somewhat raised, forming small tubercle (6). Eye oval with inner margin very shallowly sinuate, not protuberant; scattered pores without evident setae (7-9). Three ocelli present (10). Genal secretory organ absent (11). Antenna with 13 segments in male, 12 segments in female; axis of radicle not deviating much from that of scape; radicle not set into basal invagination of scape (12-14). Labio-maxillary complex slightly elongated, with glossa slightly produced and broadened; maxillary palpus 6-segmented; labial palpus 4-segmented (15-17).

MESOSOMA—Pronotum large, not much reduced mesally, freely articulating with mesothorax; hind margin shallowly arcuate; anterior "collar" well-developed; posterolateral angle rounded, reaching tegula; posteroventral margin approximately straight; ventral angle rounded, not produced (18-23). Propleura posteriorly contiguous mesally (24). Prosternum sunken except for fairly large anterior rim (25). Forecoxae very nearly contiguous (26). Mesonotum not anteriorly produced; scutellum not enlarged (27-28). Prepectus not much reduced although discontinuous midventrally, the halves considerably separated, fused to mesepisternum, the line of

fusion sulcate (29). Mesepimeron running the height of mesopleuron (30). Mesosternum essentially simple but with weak transverse carinae anteromesal to coxal cavities (31). Mid-coxae slightly separated (32). Meso- and metapleura articulating (33). Metanotum not reduced medially; metapostnotum barely discernible medially, invaginated (34-35). Endophragmal pit close to anterior margin of metapleuron; no metapleural gland (36-37). Metasternum entirely depressed, well-differentiated from mesosternum, not anteriorly produced (38-40). Hind coxae contiguous (41). Metathoracic-propodeal pleural suture entirely visible although less distinct dorsal to endophragmal pit (42). Propodeum not shortened; disc and declivity not distinct but merging (43-44). Forewing with venation not much reduced apically; ten closed cells (45-46). Pterostigma fairly large and sclerotized (47-48). Hind wing with venation not much reduced apically; two closed cells; vein C reduced distally; veins A and J absent; origin of cu-e probably distal to separation of M and Cu, not absolutely determinable; free section of Cu absent (49-53). Basal hamuli dispersed along margin, not clustered (54). Plical lobe barely indicated; short jugal lobe present (55-56). Legs slender, generally unmodified; arolia well-developed; claws toothed (57-59). Foretibia with single calcar almost straight, not highly modified (60). Mid-tibia with scattered moderate spines; two simple spurs (spurs flattened and marginally serrate in female) (61, 63-65). Hind coxa with well-developed dorsal carina (66). Hind tibia with scattered moderate spines; two simple spurs (spurs flattened and marginally serrate in female) (62, 64, 67-68).

METASOMA—No specialized "felt lines" or stridulatory apparatus (70-71). First segment neither apically constricted nor petiolate; first tergum with lateral margin



overlying sternum, not fused to it; first sternum not depressed, not highly differentiated from second (72-76). Second segment not apically constricted (77). Female with seventh tergum hidden, reduced but continuously sclerotized anteriorly; no articulation within section I of gonocoxite IX; no valve on gonapophysis VIII; gonapophysis IX moderately curved with apex directed obliquely downward (78-81). Male with seventh sternum somewhat reduced but not hidden; hypopygium simple, unmodified, not hidden; cercus present; gonapophyses IX with notum desclerotized, gonapophyses linked by membrane basally only (82-86).

FINAL INSTAR LARVA—Mandible bidentate (87). Ten pairs of fully developed spiracles (88) (data for *Sapyga* only).

BEHAVIORAL FORMULA—V<sub>a</sub>P<sub>a</sub>O (89-92)

### 13. *Myrmosid* group.

MATERIAL EXAMINED: *Myrmosa bradleyi* (♀); *M. frater* (♂); *M. melanocephala* (♂, ♀); *M. nigriceps* (♂); *M. nocturna* (♂); *M. unicolor* (♂, ♀); *Myrmosula parvula* (♂, ♀); *M. rutilans* (♀); *Protomotilla microsoma* (♀). ("Myrmosinae" of the "Tiphidae")

(Data also from Bischoff, 1915; Bridwell, 1920; Krombein, 1940; Pate, 1947a & b; Suárez, 1960; Wasbauer, 1973; Brothers, 1974b.)

GENERAL—Sexual dimorphism considerable although male not more slender than female; male winged, female apterous (1-2). No sterile caste (3). All pubescence simple (4).

HEAD—Clypeus of moderate size; antennae inserted fairly low on face (5). Antennal socket with dorsomesal rim much produced, forming well-developed tubercle (6). Eye oval with inner margin very shallowly sinuate, not protuberant; many scattered pores with moderately long setae (7-9). Three ocelli present (10). Genal

secretory organ absent (11). Antenna with 13 segments in male, 12 segments in female; axis of radicle perpendicular to that of scape; radicle set into basal invagination of scape (12-14). Labio-maxillary complex not elongated; maxillary palpus 6-segmented; labial palpus 4-segmented (15-17).

MESOSOMA—Pronotum large, not much reduced mesally, freely articulating with mesothorax; hind margin shallowly arcuate; anterior "collar" well-developed; posterolateral angle rounded, reaching tegula; posteroventral margin approximately straight; ventral angle rounded, not produced (18-23). Propleura posteriorly contiguous mesally (24). Prosternum sunken except for anterior rim (25). Forecoxae contiguous (26). Mesonotum barely anteriorly produced; scutellum not much enlarged (27-28). Prepectus not much reduced although discontinuous midventrally, the halves considerably separated, fused to mesepisternum, the line of fusion only marked by two pits ventrally (29). Mesepimeron running the height of mesopleuron (30). Mesosternum essentially simple but with weak transverse carinae anteromesal to coxal cavities (31). Midcoxae very nearly contiguous (32). Meso- and metapleura articulating (33). Metanotum not reduced medially; metapostnotum barely discernible medially, invaginated (34-35). Metepisternum and metepimeron slightly expanded anterior to endophragmal pit so that pit is shifted slightly posteriorly; no metapleural gland (36-37). Metasternum entirely depressed, well-differentiated from mesosternum, not anteriorly produced (38-40). Hind coxae contiguous (41). Metathoracic-propodeal pleural suture almost entirely obliterated, position barely discernible (42). Propodeum not shortened; disc and declivity not distinct but merging (43-44). Forewing with venation not much reduced apically; ten closed cells (45-46). Ptero-

stigma fairly large and sclerotized (47-48). Hind wing with venation not much reduced apically; two closed cells; vein C reduced distally; veins A and J absent; origin of cu-e probably distal to separation of M and Cu, not absolutely determinable; free section of Cu absent (49-53). Basal hamuli clustered near point of separation of veins C and SC+R+S (54). Plical lobe barely indicated; short jugal lobe present (55-56). Legs slender, unmodified; arolia well-developed (reduced in female); claws toothed (simple in female) (57-59). Fore-tibia with single calcar almost straight, not highly modified (60). Mid-tibia with scattered moderate spines; two simple spurs (spurs flattened and marginally serrate in female) (61, 63-65). Hind coxa with lamellate dorsal carina (66). Hind tibia with scattered moderate spines; two simple spurs (spurs flattened and marginally serrate in female) (62, 64, 67-68). Modified mesosoma of female with pronotum large, articulating with mesothorax; prepectal sclerite fused to mesepisternum; meso- and metathorax and propodeum fused completely dorsally; pleura with only meso-metapleural suture faintly visible, flattened (69).

**METASOMA**—No specialized "felt lines" (70). Stridulitrum present as a single small shield-shaped area medially at base of third tergum (71). First segment neither apically constricted nor petiolate (slightly constricted in male); first tergum with lateral margin overlying sternum, not fused to it; first sternum posteriorly depressed, separated from second by a deep constriction (72-76). Second segment not apically constricted (77). Female with seventh tergum hidden, reduced but continuously sclerotized anteriorly; no articulation within section I of gonocoxite IX; valve present on gonapophysis VIII; gonapophysis IX considerably curved, especially basally, with apex directed downward (78-81). Male with seventh sternum

not reduced nor hidden; hypopygium simple but concealed; cercus present; gonapophyses IX with notum desclerotized, gonapophyses linked by membrane basally only (82-86).

**FINAL INSTAR LARVA**—Mandible quadridentate (87). Nine pairs of fully developed spiracles, i.e., second pair reduced (88) (pers. obs.).

**BEHAVIORAL FORMULA**— $V_a P_a OC$  (89-92).

#### 14. *Mutillid group.*

**MATERIAL EXAMINED:** Specimens of approximately 150 genera and subgenera. (See section on Mutillidae below, Table III, for complete list.) ("Pseudophotopsidinae - Sphaerophthalminae - Mutillinae - Rhopalomutillinae" of the "Mutillidae") (Data also from Bischoff, 1920-21; Mickel, 1928; Schuster, 1947, 1949; Brothers, 1972; Debolt, 1973.)

**GENERAL**—Sexual dimorphism considerable, although male not more slender than female; male winged, female apterous (1-2). No sterile caste (3). All pubescence simple (4).

**HEAD**—Clypeus of moderate size; antennae inserted fairly low on face (5). Antennal socket with dorsomesal rim much produced, forming well-developed tubercle (6). Eye oval with inner margin very shallowly sinuate, not protuberant; scattered sensory pores without evident setae (7-9). Three ocelli present (10). Genal secretory organ absent (11). Antenna with 13 segments in male, 12 segments in female; axis of radicle perpendicular to that of scape; radicle set into basal invagination of scape (12-14). Labio-maxillary complex not elongated; maxillary palpus 6-segmented; labial palpus 4-segmented (15-17).

**MESOSOMA**—Pronotum fairly large, somewhat reduced mesally; articulation with mesothorax slightly restricted but with no

fusion; hind margin concave; anterior "collar" well-developed; posterolateral angle very slightly dorsally produced anterior to tegula, thus appearing truncate but reaching tegula; posteroventral margin approximately straight; ventral angle rounded, not produced (18-23). Propleura posteriorly contiguous mesally (24). Prosternum sunken except for anterior rim (25). Forecoxae contiguous (26). Mesonotum only slightly anteriorly produced; scutellum not enlarged (27-28). Prepectus not much reduced although discontinuous midventrally, the halves considerably separated, fused to mesepisternum, the line of fusion marked by two pits ventrally (29). Mesepimeron running the height of mesopleuron although poorly differentiated ventrally (30). Mesosternum essentially simple but with weak transverse carinae anteromesal to coxal cavities (31). Mid-coxae very nearly contiguous (32). Meso- and metapleura articulating (33). Metanotum slightly reduced medially; metapostnotum barely discernible medially, invaginated (34-35). Metepisternum and metepimeron slightly expanded anterior to endophragmal pit so that pit is shifted slightly posteriorly; no metapleural gland (36-37). Sternum entirely depressed but slightly ventrally produced anteromesal to coxal cavities, well-differentiated from mesosternum, not anteriorly produced (38-40). Hind coxae contiguous (41). Metathoracic-propodeal pleural suture almost entirely obliterated, position barely discernible (42). Propodeum not shortened; disc and declivity not distinct but merging (43-44). Forewing with venation reduced apically; ten closed cells (45-46). Pterostigma fairly large and sclerotized (47-48). Hind wing with venation reduced apically; two closed cells; vein C reduced distally; veins A and J absent; cu-e apparently originating distal to separation of M and Cu; free section of Cu apparently absent (49-53). Basal

hamuli clustered near point of separation of veins C and SC+R+S (54). Plical lobe barely indicated; extremely short jugal lobe present (55-56). Legs slender, unmodified; arolia well-developed; claws toothed (57-59). Foretibia with single calcar almost straight, not highly modified (60). Mid-tibia with scattered moderate spines; two simple spurs (spurs flattened and serrate in female) (61, 63-65). Hind coxa with weak dorsal carina basally (66). Hind tibia with scattered moderate spines; two simple spurs (spurs flattened and serrate in female) (62, 64, 67-68). Modified mesosoma of female with pronotum fused to mesothorax but with suture visible; prepectus fused to mesepisternum; meso- and metathorax fused completely dorsally, with pleurointersegmental suture faintly visible laterally; metathoracic-propodeal notal and pleural sutures visible only above endophragmal pit; pleura flattened (69).

**METASOMA**—Tendency toward development of felted secretory areas ("felt lines") on second segment, on both tergum and sternum laterally (70). Stridulitrum present as a small shield-shaped area medially at base of third tergum (71). First segment neither apically constricted nor petiolate (slightly constricted in male); first tergum with lateral margin overlying sternum, not fused to it; first sternum posteriorly depressed, separated from second by a deep constriction (72-76). Second segment not apically constricted (77). Female with seventh tergum hidden, reduced but continuously sclerotized anteriorly; no articulation within section I of gonocoxite IX; valve present on gonapophysis VIII; gonapophysis IX considerably curved, especially basally, with apex directed downward (78-81). Male with seventh sternum somewhat reduced but not hidden; hypopygium simple, unmodified, not hidden; cercus present; gonapophyses IX with notum desclerotized, gonapophyses linked by membrane basally only (82-86).

FINAL INSTAR LARVA—Mandible quadridentate (87). Nine pairs of fully developed spiracles, i.e., second pair reduced (88).

BEHAVIORAL FORMULA— $V_a P_a OC$  (89-92).

### 15. *Sierolomorphid* group.

MATERIAL EXAMINED: *Sierolomorpha* ?*apache* ( $\delta$ ); *S. canadensis* ( $\delta$ ,  $\varphi$ ); *S. nigrescens* ( $\delta$ ,  $\varphi$ ); *S. similis* ( $\delta$ ). ("Sierolomorphidae")

(Data also from Evans, 1961; Nagy, 1971.)

GENERAL—Sexual dimorphism minimal, both sexes of similar form and fully winged (1-2). No sterile caste (3). All pubescence simple (4).

HEAD—Clypeus of moderate size; antennae inserted low on face (5). Antennal socket simple but with dorsomesal rim very slightly raised, no true tubercle (6). Eye oval with inner margin very shallowly sinuate, not protuberant; scattered pores with short setae (7-9). Three ocelli present (10). Genal secretory organ absent (11). Antenna with 13 segments in male, 12 segments in female; axis of radicle not deviating much from that of scape; radicle not set into basal invagination of scape (12-14). Labio-maxillary complex not elongated; maxillary palpus 6-segmented; labial palpus 4-segmented (15-17).

MESOSOMA—Pronotum large, not reduced mesally, freely articulating with mesothorax; hind margin shallowly arcuate (somewhat more deeply so in male); anterior "collar" well-developed; posterolateral angle rounded, reaching tegula; posteroventral margin slightly concave; ventral angle rounded, not produced (18-23). Propleura posteriorly contiguous mesally (24). Prosternum sunken except for anterior rim (25). Forecoxae contiguous (26). Mesonotum not anteriorly produced (very slightly produced in male); scutellum not enlarged (27-28). Prepectus not fused to mesepisternum, discontinuous midventrally, the halves considerably separated

(29). Mesepimeron running the height of mesopleuron (30). Mesosternum essentially simple but with weak ridges anteromesal to coxal cavities (31). Mid-coxae slightly separated (32). Metanotum not reduced medially; metapostnotum visible medially, slightly depressed but not invaginated (33-34). Metepimeron slightly expanded anteroventral to endophragmal pit so that pit is a short distance from anterior margin of metapleuron; no metapleural gland (35-36). Metasternum entirely depressed except for slight ridges anterior to coxae, well-differentiated from mesosternum, not anteriorly produced (38-40). Hind coxae contiguous (41). Metathoracic-propodeal pleural suture barely discernible dorsal to endophragmal pit, not visible ventrally (42). Propodeum not shortened; disc and declivity somewhat distinct although merging (43-44). Forewing with venation reduced apically; seven closed cells; vein S absent between its separation from M and junction with r-s; crossveins 2s-m and 2m-cu absent (45-46). Pterostigma large and sclerotized (47-48). Hind wing with venation reduced apically; two closed cells; vein C reduced distally; veins A and J absent; cu-c originating proximal to separation of M and Cu; free section of Cu present (49-53). Basal hamuli dispersed along margin although tending toward concentration at separation of vein SC+R+S from margin (54). Plical lobe barely indicated; jugal lobe absent (55-56). Legs slender, generally unmodified; arolia well-developed; claws toothed (57-59). Foretibia with single calcar almost straight, not highly modified (60). Mid-tibia with scattered weak spines; two simple spurs (61, 63-65). Hind coxa with weak dorsal carina (66). Hind tibia with scattered weak spines; two simple spurs (62, 64, 67-68).

METASOMA—No specialized "felt lines" or stridulatory apparatus (70-71). First segment neither apically constricted nor peti-

olate; first tergum with lateral margin overlying sternum, not fused to it; first sternum not depressed, not highly differentiated from second (72-76). Second segment not apically constricted (77). Female with seventh tergum hidden, reduced but continuously sclerotized anteriorly; no articulation within section 1 of gonocoxite IX; valve present on gonapophysis VIII; gonapophysis IX gently curved, almost straight, with apex only weakly directed obliquely downward (78-81). Male with seventh sternum not reduced nor hidden; hypopygium reduced, very narrow, hidden except for extreme apex; cercus present; gonapophyses IX with notal fusion well-developed, especially basally (82-86).

LARVA—Unknown.

BEHAVIORAL FORMULA—Unknown.

#### 16. *Pompilid group.*

MATERIAL EXAMINED: *Anoplius amethystinus* ( $\delta$ ,  $\varphi$ ); *Ceropales maculata* ( $\delta$ ,  $\varphi$ ); *Chirodamnus pyrromelas* ( $\varphi$ ); *Cryptochelilus severini* ( $\delta$ ,  $\varphi$ ); *Episyrus quinquenotatus* ( $\delta$ ,  $\varphi$ ); *Euclavelia fasciata* ( $\varphi$ ); *Evagetes parvus* ( $\delta$ ,  $\varphi$ ); *Paracyphononyx funereus* ( $\delta$ ,  $\varphi$ ); *Pepsis thisbe* ( $\delta$ ,  $\varphi$ ); *Poecilopompilus interruptus* ( $\delta$ ,  $\varphi$ ); *Pompilus scelestus* ( $\delta$ ,  $\varphi$ ); *Psorthaspis connexa* ( $\delta$ ,  $\varphi$ ); *Tachypompilus ferrugineus* ( $\delta$ ,  $\varphi$ ). ("Pompilidae")

(Data also from Evans, 1953, 1959b, 1972; Daly, 1955.)

GENERAL—Sexual dimorphism minimal, male slightly smaller than female but of similar form; both sexes fully winged (1-2). No sterile caste (3). All pubescence simple (4).

HEAD—Clypeus of moderate size; antennae inserted fairly low on face (5). Antennal socket simple, without tubercle (6). Eye oval with inner margin shallowly sinuate, not protuberant; scattered pores without evident setae (7-9). Three ocelli present (10). Genal secretory organ ab-

sent (11). Antenna with 13 segments in male, 12 segments in female; axis of radicle not deviating much from that of scape; radicle not set into basal invagination of scape (12-14). Labio-maxillary complex not elongated; maxillary palpus 6-segmented; labial palpus 4-segmented (15-17).

MESOSOMA—Pronotum large, not mesally reduced, freely articulating with mesothorax; hind margin arcuate; anterior "collar" well-developed; posterolateral angle rounded, reaching tegula; posteroventral margin slightly concave; ventral angle rounded, not produced (18-23). Propleura posteriorly contiguous mesally (24). Prosternum sunken except for anterior rim (25). Forecoxae contiguous (26). Mesonotum not anteriorly produced; scutellum not enlarged (27-28). Prepectus not much reduced although discontinuous midventrally, the halves considerably separated, fused to mesepisternum, the line of fusion retained as a sulcus (29). Mesepimeron running the height of mesopleuron (30). Mesosternum essentially simple but with weak ridges anteromesal to coxal cavities (31). Mid-coxae contiguous (32). Mesosoma and metapleura not mutually movable although not fused (33). Metanotum not reduced medially; metapostnotum well-developed, visible medially, slightly depressed but not invaginated (34-35). Metepimeron slightly expanded anteroventral to endophragmal pit so that pit is a short distance from anterior margin of metapleuron; no metapleural gland (36-37). Metasternum entirely depressed except for slight ridges anterior to coxae, well differentiated from mesosternum, not anteriorly produced (38-40). Hind coxae contiguous (41). Metathoracic-propodeal pleural suture entirely visible (42). Propodeum not shortened; disc and declivity somewhat distinct although merging (43-44). Forewing with venation not reduced apically; ten closed cells (45-46). Pterostigma fairly

small with sclerotization reduced (47-48). Hind wing with venation not reduced apically; two closed cells; vein C reduced distally; veins A and J absent; cu-c originating proximal to separation of M and Cu; free section of Cu present (49-53). Basal hamuli strongly concentrated into a basal cluster at separation of vein SC+R+S from margin (54). Plical lobe barely indicated; moderate jugal lobe present (55-56). Legs slender, generally unmodified although somewhat elongated; arolia well-developed; claws toothed (57-59). Foretibia with single calcar almost straight, not highly modified (60). Midtibia with scattered moderate spines; two spurs slightly dorsally flattened (61, 63-65). Hind coxa simple (66). Hind tibia with scattered moderate spines; two spurs slightly dorsally flattened, the inner one modified as a calcar by development of basal brush of setae dorsally (62, 64, 67-68).

**METASOMA**—No specialized "felt lines" or stridulatory apparatus (70-71). First segment neither apically constricted nor petiolate; first tergum with lateral margin overlying sternum, not fused to it; first sternum not depressed, not highly differentiated from second (72-76). Second segment not apically constricted (77). Female with seventh tergum hidden, reduced but continuously sclerotized anteriorly; no articulation within section I of gonocoxite IX; no valve on gonapophysis VIII; gonapophysis IX gently curved, almost straight, with apex only weakly directed obliquely downward (78-81). Male with seventh sternum reduced but not hidden; hypopygium essentially simple, not reduced nor hidden; cercus present; gonapophyses IX with notal fusion well-developed (82-86).

**FINAL INSTAR LARVA**—Mandible tridentate (87). Nine pairs of fully developed spiracles, i.e., second pair reduced (88).

**BEHAVIORAL FORMULA**— $V_a P_a T_a OC$  (89-92).

### 17. *Rhopalosomatid* group.

**MATERIAL EXAMINED:** *Olixon banksii* (♂, ♀); *O. testaceum* (♀); ?*Olixon* sp. (♂, Cameroon); *Rhopalosoma* spp. (♀; Madagascar, Panama). ("Rhopalosomatidae") (Data also from Perkins, 1908; Reid, 1939; Brues, 1943; Gurney, 1953.)

**GENERAL**—Sexual dimorphism minimal, male slightly smaller than female but of similar form; both sexes fully winged (1-2). No sterile caste (3). All pubescence simple (4).

**HEAD**—Clypeus of moderate size; antennae inserted fairly low on face (5). Antennal socket simple, without tubercle (6). Eye oval with inner margin shallowly sinuate, not protuberant; scattered pores with short setae (7-9). Three ocelli present (10). Genal secretory organ absent (11). Antenna with 13 segments in male, 12 segments in female; axis of radicle not deviating much from that of scape; radicle not set into basal invagination of scape (12-14). Labio-maxillary complex not elongated; maxillary palpus 6-segmented; labial palpus 4-segmented (15-17).

**MESOSOMA**—Pronotum somewhat reduced mesally, fairly freely articulating with mesothorax; hind margin concave; anterior "collar" fairly well-developed; posterolateral angle rounded, very slightly produced dorsally and thus truncate although reaching tegula; posteroventral margin slightly concave; ventral angle rounded, not produced (18-23). Propleura posteriorly contiguous mesally (24). Prosternum sunken except for anterior rim (25). Forecoxae contiguous (26). Mesonotum somewhat anteriorly produced; scutellum not enlarged (27-28). Prepectus not fused to mesepisternum, much reduced, short and tall, hidden under pronotum, discontinuous midventrally, the halves considerably separated (29). Mesepimeron running the height of mesopleuron (30). Mesosternum with platelike

projections posteromesally over coxal cavities (31). Mid-coxae contiguous (32). Meso- and metapleura articulating (33). Metanotum not reduced medially; metapostnotum visible medially, depressed but not invaginated (34-35). Metepimeron somewhat expanded anteroventral to endophragmal pit so that pit is some distance from anterior margin of metapleuron; no metapleural gland (36-37). Metasternum entirely depressed, well-differentiated from mesosternum, not anteriorly produced (38-40). Hind coxae contiguous (41). Metathoracic-propodeal pleural suture entirely visible (42). Propodeum not shortened; disc and declivity not distinct but merging (43-44). Forewing with venation slightly reduced apically; eight closed cells, including cell C which is much reduced by fusion of veins C and SC+R+S except distally; crossveins 2s-m and 2m-cu absent (45-46). Pterostigma small with sclerotization reduced (47-48). Hind wing with venation slightly reduced apically; two closed cells; vein C reduced distally; veins A and J absent; cu-e originating proximal to separation of M and Cu; free section of Cu present (49-53). Basal hamuli strongly concentrated into a basal cluster at separation of vein SC+R+S from margin (54). Plical lobe well-marked by a deep incision; moderate jugal lobe present (55-56). Legs slender, little modified (tarsi flattened and broadened, forefemur swollen and arolia enlarged in female); arolia well-developed; claws toothed (57-59). Foretibia with single calcar almost straight, not highly modified (60). Mid-tibia with scattered weak spines; two simple spurs (61, 63-65). Hind coxa simple (66). Hind tibia with scattered weak spines; two simple spurs, the inner one modified as a calcar by development of basal brush of setae dorsally (62, 64, 67-68).

**METASOMA**—No specialized "felt lines" or stridulatory apparatus (70-71). First segment apically somewhat constricted, not

petiolate; first tergum with lateral margin overlying sternum, not fused to it; first sternum not depressed although fairly well-differentiated from second (72-76). Second segment not apically constricted (77). Female with seventh tergum hidden, reduced but continuously sclerotized anteriorly; no articulation within section 1 of gonocoxite IX; valve present on gonapophysis VIII; gonapophysis IX gently curved, with apex directed obliquely upward (78-81). Male with seventh sternum reduced but not hidden; hypopygium essentially simple, not reduced nor hidden; cercus present; gonapophyses IX with notal fusion well-developed (82-86).

**FINAL INSTAR LARVA**—Mandible essentially unidentate (inner margin serrate) (87). Ten pairs of fully developed spiracles (88).

**BEHAVIORAL FORMULA**— $V_a(P_a?)O$  (89-92).

### 18. *Formicid* group.

**MATERIAL EXAMINED:** *Aphaenogaster fulva* ( $\delta, \text{♀}, \text{♀}$ ); *Atta cephalotes* ( $\delta, \text{♀}, \text{♀}$ ); *Camponotus herculeanus* ( $\delta, \text{♀}, \text{♀}$ ); *Crematogaster coarctata* ( $\delta, \text{♀}, \text{♀}$ ); *Dinoponera* sp. ( $\text{♀}$ , Argentina); *Eciton vagans* ( $\delta, \text{♀}$ ); *Ectatomma tuberculatum* ( $\delta, \text{♀}, \text{♀}$ ); *Labidus coecus* ( $\delta, \text{♀}$ ); *Liometopium apiculatum* ( $\delta, \text{♀}, \text{♀}$ ); *Myrmecia* spp. ( $\text{♀}$ , Queensland); *Neoponera villosa* ( $\text{♀}, \text{♀}$ ); *Nomamyrmex crassicornis* ( $\delta, \text{♀}$ ); *Odontomachus haematoda* ( $\delta, \text{♀}$ ); *Paltothyreus* sp. ( $\delta, \text{♀}, \text{♀}$ ; Mozambique); *Paraponera clavata* ( $\delta, \text{♀}, \text{♀}$ ); *Pogonomyrmex barbatus* ( $\delta, \text{♀}, \text{♀}$ ). ("Formicidae")

(Data also from Haskins & Ensmann, 1938; Brown & Nutting, 1950; Creighton, 1950; Haskins & Haskins, 1950; Wheeler & Wheeler, 1952, 1971; Brown, 1954, 1969; Brown & Wilson, 1959; Hermann & Blum, 1966; Wilson, Carpenter & Brown, 1967; Gotwald, 1969; Wilson, 1971; Markl, 1973.)

**GENERAL**—Sexual dimorphism moderate,

male somewhat smaller but not much more slender than female; both sexes fully winged (1-2). Wingless sterile female worker caste present (3). All pubescence simple (4).

**HEAD**—Clypeus of moderate size; antennae inserted low on face (5). Antennal socket simple, without tubercle (6). Eye oval with inner margin shallowly sinuate, not protuberant; scattered pores with short setae (7-9). Three ocelli present (10). Genal secretory organ absent (11). Antenna with 13 segments in male, 12 segments in female; axis of radicle not deviating much from that of scape; radicle set into basal invagination of scape (12-14). Labio-maxillary complex not elongated; maxillary palpus 6-segmented; labial palpus 4-segmented (15-17).

**MESOSOMA**—Pronotum large, somewhat reduced mesally, fairly freely articulating with mesothorax; hind margin deeply arcuate; anterior "collar" well-developed; posterolateral angle very slightly dorsally produced posteriorly, thus appearing truncate although reaching tegulae; posteroventral margin slightly concave; ventral angle acute, somewhat mesally produced (18-23). Propleura posteriorly contiguous mesally (24). Prosternum sunken except for anterior rim (25). Forecoxae contiguous (26). Mesonotum slightly anteriorly produced; scutellum not enlarged (27-28). Prepectus fused to mesepisternum, not distinguishable, apparently very short and narrow, hidden under pronotum (29). Mesepimeron reduced, distinguishable only at dorsal extreme (30). Mesosternum simple, without posterior projections (31). Mid-coxae slightly separated (32). Meso- and metapleura fused, not mutually movable (possibly not fused in *Sphecomyrma*) (33). Metanotum not reduced medially; metapostnotum not visible medially, invaginated (34-35). Metepisternum and metepimeron expanded anterior to endophragmal pit so that pit is some distance

from anterior margin of metapleuron; metapleural gland present, opening above hind coxa (36-37). Metasternum entirely depressed, well-differentiated from mesosternum, not anteriorly produced (38-40). Hind coxae contiguous (41). Metathoracic-propodeal pleural suture entirely distinguishable (42). Propodeum not shortened; disc and declivity not distinct but merging (43-44). Forewing with venation not much reduced apically; eight closed cells; veins 2s-m and 2m-cu absent (45-46). Pterostigma moderate and sclerotized (47-48). Hind wing with venation not much reduced apically; two closed cells; vein C reduced distally; veins A and J absent; cu-e originating proximal to separation of M and Cu; free section of Cu present (49-53). Basal hamuli absent (54). Plical lobe indicated by a shallow notch; moderate jugal lobe present (55-56). Legs slender, generally unmodified; arolia well-developed; claws toothed (57-59). Foretibia with single calcar almost straight, not much modified (60). Mid-tibia with few moderate spines apically only; two spurs, the inner dorsally carinate-pectinate forming a calcar, the outer simple (61, 63-65). Hind coxa simple (66). Hind tibia with few moderate spines apically only; two spurs, the inner dorsally carinate-pectinate forming a calcar, the outer simple (62, 64, 67-68).

**METASOMA**—No specialized "felt lines" or stridulatory apparatus (70-71). First segment somewhat apically constricted, not petiolate; first tergum with lateral margin overlying sternum, not fused to it; first sternum slightly depressed, differentiated from second by a slight constriction (72-76). Second segment not apically constricted (77). Female with seventh tergum hidden, reduced but continuously sclerotized anteriorly; no articulation within section I of gonocoxite IX; valve present on gonapophysis VIII; gonapophysis IX almost straight, with apex weakly directed



obliquely upward (78-81). Male with seventh sternum not reduced nor hidden; hypopygium simple, unmodified, not hidden; cercus present; gonapophyses IX with notal fusion well-developed (82-86).

FINAL INSTAR LARVA—Mandible tridentate (87). Ten pairs of fully developed spiracles (88).

BEHAVIORAL FORMULA— $I[IO^n(V_aP_aT_a)^x]^i$  (89-92).

### 19. *Scoliid* group.

MATERIAL EXAMINED: *Austroscolia nitida* ( $\delta$ ); *Campsomeris marginella* ( $\delta$ ,  $\text{♀}$ ); *Scolia nobilitata* ( $\delta$ ,  $\text{♀}$ ); *Trielis octomaculata* ( $\delta$ ,  $\text{♀}$ ); *Trisciloa zonata* ( $\delta$ ). ("Scoliidae")

(Data also from Betrem, 1928; Bradley, 1950; Grandi, 1961; Iuga, 1968.)

GENERAL—Sexual dimorphism slight, male only slightly more slender than female; both sexes fully winged (1-2). No sterile caste (3). All pubescence simple (4).

HEAD—Clypeus somewhat enlarged; antennae inserted moderately high on face (somewhat higher in male) (5). Antennal socket simple, without tubercle (6). Eye oval with inner margin deeply incised, not protuberant; pores and setae absent (7-9). Three ocelli present (10). Genal secretory organ absent (11). Antenna with 13 segments in male, 12 segments in female; axis of radicle not deviating much from that of scape; radicle not set into basal invagination of scape (12-14). Labio-maxillary complex somewhat elongated, with both glossa and paraglossa produced; maxillary palpus 6-segmented; labial palpus 4-segmented (15-17).

MESOSOMA—Pronotum considerably reduced and short mesally, not freely movable against mesothorax but tightly appressed to it; hind margin strongly concave; anterior "collar" well-developed; posterolateral angle slightly produced

above tegula, thus appearing notched but reaching tegula; posteroventral margin strongly concave; ventral angle acute, somewhat produced (18-23). Propleura posteriorly contiguous mesally (24). Prosternum entirely sunken, without differentiated anterior rim (25). Forecoxae contiguous (26). Mesonotum enlarged and anteriorly produced; scutellum not enlarged (27-28). Prepectus fused to mesepisternum, much reduced but tall, discontinuous midventrally, the halves considerably separated, hidden under pronotum (29). Mesepimeron running the height of mesopleuron although pleural sulcus much reduced and not differentiated externally (30). Mesosternum flat, laterally broadened, with small plate-like projections over coxal cavities (31). Midcoxae very broadly separated (32). Meso- and metapleura not mutually movable although not fused (33). Metanotum not reduced medially; metapostnotum not visible medially, invaginated (34-35). Endophragmal pit a short distance from anterior margin of metapleuron and metepisternum posteriorly expanded; no metapleural gland (36-37). Metasternum large, laterally broadened, with small plate-like projections over coxal cavities, little differentiated from mesosternum but not anteriorly produced (38-40). Hind coxae broadly separated (41). Metathoracic-propodeal pleural suture entirely distinct (42). Propodeum not much shortened; disc and declivity fairly distinct (43-44). Forewing with venation reduced apically; ten closed cells (45-46). Pterostigma reduced and partially desclerotized (47-48). Hind wing with venation reduced apically; three closed cells; veins A and J absent; cu-e originating proximal to separation of M and Cu; free section of Cu present (49-53). Basal hamuli absent (54). Plical lobe not indicated; long jugal lobe indicated by a deep incision (55-56). Legs fairly slender, unmodified (stouter in female

with femora and tibiae somewhat enlarged); arolia well-developed; claws simple (57-59). Foretibia with single calcar slightly curved, posteriorly hollowed and spatulate (60). Mid-tibia with scattered stout spines; one spur, slightly dorsally flattened (61, 63-65). Hind coxa simple (66). Hind tibia with scattered stout spines; two slightly flattened spurs (62, 64, 67-68).

**METASOMA**—No specialized "felt lines" or stridulatory apparatus (70-71). First segment slightly apically constricted, not petiolate; first tergum with lateral margin overlying sternum, not fused to it; first sternum entirely depressed, highly differentiated from the second by a marked constriction (72-76). Second segment not constricted apically (77). Female with seventh tergum hidden, reduced but continuously sclerotized anteriorly; no articulation within section I of gonocoxite IX; valve present on gonapophysis VIII; gonapophysis IX moderately curved, with apex directed obliquely downward (78-81). Male with seventh sternum neither reduced nor hidden; hypopygium apically produced as three subequal spines, almost entirely concealed (except only for tips of spines); cercus absent; gonapophyses IX with notum desclerotized, gonapophyses linked by membrane along most of their length (82-86).

**FINAL INSTAR LARVA**—Mandible tridentate (87). Ten pairs of fully developed spiracles (88).

**BEHAVIORAL FORMULA**— $V_n P_n (? T_n) O$  (89-92).

## 20. *Vespid* group.

**MATERIAL EXAMINED:** *Ancistrocerus antilope* ( $\delta$ ,  $\varphi$ ); *Belonogaster* spp. ( $\delta$ , Uganda;  $\varphi$ , South Africa); *Brachygastra lecheguana* ( $\delta$ ,  $\varphi$ ); *Ceramius bicolor* ( $\delta$ ,  $\varphi$ ); *C. lichtensteini* ( $\delta$ ,  $\varphi$ ); *Eumenes fraternus* ( $\delta$ ,  $\varphi$ ); *Euodynerus annulatus*

( $\delta$ ,  $\varphi$ ); *Euparagia scutellaris* ( $\delta$ ,  $\varphi$ ); *E. timberlakai* ( $\delta$ ,  $\varphi$ ); *Monobia quadridens* ( $\delta$ ,  $\varphi$ ); *Polistes metricus* ( $\delta$ ,  $\varphi$ ); *Polybia sericea* ( $\varphi$ ); *Provespa barthelemyi* ( $\delta$ ,  $\varphi$ ); *Pseudomasaris vespoides* ( $\delta$ ,  $\varphi$ ); *Pterocheilus quinquefasciatum* ( $\delta$ ,  $\varphi$ ); *Stenodynerus papagorum* ( $\delta$ ,  $\varphi$ ); *Symmorphus canadensis* ( $\delta$ ,  $\varphi$ ); *Synagris cornuta* ( $\delta$ ); *Synoeca surinama* ( $\varphi$ ); *Vespa crabro* ( $\delta$ ,  $\varphi$ ); *Vespula norvegicoides* ( $\delta$ ,  $\varphi$ ); *Zethus matzicatzin* ( $\delta$ ,  $\varphi$ ). ("Masaridae," "Eumenidae," "Vespidae") (Data also from Duncan, 1939; Reid, 1942; Grandi, 1961; Richards, 1962; Evans, 1966; Torchio, 1970; Charnley, 1973.)

**GENERAL**—Sexual dimorphism minimal, male not much more slender than female; both sexes fully winged (1-2). No sterile caste (3). All pubescence simple (4).

**HEAD**—Clypeus somewhat enlarged; antennae inserted moderately high on face (5). Antennal socket simple, without tubercle (6). Eye oval with inner margin fairly deeply incised, not protuberant; scattered pores without evident setae (7-9). Three ocelli present (10). Genal secretory organ absent (11). Antenna with 13 segments in male, 12 segments in female; axis of radicle not deviating much from that of scape; radicle not set into basal invagination of scape (12-14). Labio-maxillary complex slightly elongated, with both glossa and paraglossa somewhat produced; maxillary palpus 6-segmented; labial palpus 4-segmented (15-17).

**MESOSOMA**—Pronotum extremely reduced and short mesally, not freely movable against mesothorax but tightly appressed to it; hind margin strongly concave; anterior "collar" slightly reduced; posterolateral angle slightly produced above tegula and exceeding its anterior margin, the angle thus appearing acute; posteroventral margin strongly concave; ventral angle acute, slightly ventrally produced (18-23). Propleura posteriorly contiguous mesally

(24). Prosternum entirely sunken, without differentiated anterior rim (25). Forecoxae contiguous (26). Mesonotum enlarged and anteriorly produced; scutellum not enlarged (27-28). Prepectus not fused to mesepisternum, much reduced, very short, discontinuous midventrally, the halves very considerably separated, hidden under pronotum (29). Mesepimeron running the height of mesopleuron although much reduced (30). Mesosternum essentially simple but with anteromesal rims of coxal cavities acutely produced posteriorly (31). Mid-coxae contiguous (32). Meso- and metapleura not mutually movable although apparently not fused (33). Metanotum not reduced medially; metapostnotum not visible medially, invaginated (34-35). Metepisternum and metepimeron expanded anterior to endophragmal pit so that pit is some distance from anterior margin of metapleuron; no metapleural gland (36-37). Metasternum entirely depressed except for anteromesal ridge, to accommodate mid-coxae, well-differentiated from mesosternum, not anteriorly produced (38-40). Hind coxae contiguous (41). Metathoracic-propodeal pleural suture entirely distinct (42). Propodeum shortened dorso-medially so that disc virtually absent, merging with declivity (43-44). Forewing with venation not much reduced apically; ten closed cells (45-46). Pterostigma fairly small and slightly desclerotized (47-48). Hind wing with venation not much reduced apically; three closed cells; veins A and J absent; cu-e originating proximal to separation of M and Cu; free section of Cu present (49-53). Basal hamuli absent (54). Plical lobe barely indicated; moderate jugal lobe present (55-56). Legs slender, unmodified; arolia well-developed; claws toothed (57-59). Foretibia with single calcar almost straight, not much modified (60). Mid-tibia with scattered weak spines; two simple spurs (61,

63-65). Hind coxa simple (66). Hind tibia with scattered weak spines; two spurs, the inner carinate and fringed dorsally, forming a calcar, the outer simple (62, 64, 67-68).

**METASOMA**—No specialized "felt lines" or stridulatory apparatus (70-71). First segment neither apically constricted nor petiolate; first tergum with lateral margin overlying sternum, not fused to it; first sternum depressed, especially posteriorly, highly differentiated from second by a marked constriction (72-76). Second segment not apically constricted (77). Female with seventh tergum hidden, reduced but continuously sclerotized anteriorly; no articulation within section 1 of gonocoxite IX; no valve on gonapophysis VIII; gonapophysis IX almost straight, with apex only weakly directed obliquely downward (78-81). Male with seventh sternum reduced although not entirely hidden; hypopygium simple, unmodified, not hidden; cercus absent; gonapophyses IX with notal fusion well-developed (82-86).

**FINAL INSTAR LARVA**—Mandible tridentate (87). Ten pairs of fully developed spiracles (88).

**BEHAVIORAL FORMULA**—IO(V<sub>a</sub>P<sub>a</sub>T<sub>a</sub>)<sup>n</sup>C (89-92).

### 21. *Eotillid* group.

**MATERIAL EXAMINED:** *Eotilla mickeli* (♂, ♀); *E. superba* (♂). ("Eotillinae" of the "Mutillidae")

(Data also from Schuster, 1949; Mickel, 1968.)

**GENERAL**—Sexual dimorphism considerable, male not much more slender than female; male winged, female apterous (1-2). No sterile caste (3). Much pubescence of sub-plumose setae and plumose scales (4).

**HEAD**—Clypeus of moderate size; antennae inserted fairly low on face (5). Antennal socket simple, without tubercle (6). Eye oval with inner margin very shallowly

sinuate, not protuberant; scattered pores with short setae (7-9). Three ocelli present (absent in female) (10). Genal secretory organ absent (11). Antenna with 13 segments in male, 12 segments in female; axis of radicle not deviating much from that of scape; radicle not set into basal invagination of scape (12-14). Labio-maxillary complex not elongated; maxillary palpus 6-segmented; labial palpus 4-segmented (15-17).

**MESOSOMA**—Pronotum large, very little reduced medially, freely articulating with mesothorax; hind margin arcuate; anterior "collar" well-developed; posterolateral angle rounded, reaching tegula; posteroventral margin approximately straight; ventral angle rounded, not produced (18-23). Propleura posteriorly contiguous mesally (24). Prosternum sunken except for anterior rim (25). Forecoxae nearly contiguous (26). Mesonotum not much anteriorly produced; scutellum not enlarged (27-28). Prepectus not fused to mesepisternum (probably—not determinable without dissection), discontinuous midventrally, the halves considerably separated, very short and tall (29). Mesepimeron reduced, distinguishable only at dorsal extreme (30). Mesosternum simple, without posterior projections (31). Midcoxae somewhat separated (32). Meso- and metapleura not mutually movable although not fused (33). Metanotum not reduced medially; metapostnotum not visible medially, invaginated (34-35). Metepimeron very slightly expanded anteroventral to endophragmal pit so that pit is a short distance from anterior margin of metapleuron; no metapleural gland (36-37). Metasternum depressed only laterally to accommodate mid-coxae, mesally little differentiated from mesosternum and slightly anteriorly produced (38-40). Hind coxae contiguous (41). Metathoracic-propodeal pleural suture visible dorsal to endophragmal pit, not distinguishable ven-

trally (42). Propodeum not shortened; disc and declivity somewhat distinct although merging (43-44). Forewing with venation reduced apically; ten closed cells (45-46). Pterostigma fairly large and sclerotized (47-48). Hind wing with venation reduced apically; two closed cells; vein C reduced distally; veins A and J absent; cu-e originating proximal to separation of M and Cu; free section of Cu present (49-53). Basal hamuli strongly clustered at separation of vein SC+R+S from margin (54). Plical lobe well-marked by a deep incision; moderate jugal lobe present (55-56). Legs slender, generally unmodified; arolia reduced; claws toothed (57-59). Foretibia with single calcar almost straight, not highly modified (60). Mid-tibia with scattered weak spines; two simple spurs (61, 63-65). Hind coxa with weak dorsal carina basally (66). Hind tibia with scattered weak spines; two simple spurs (62, 64, 67-68). Modified mesosoma of female with pronotum large, articulating with mesothorax; mesonotum extremely short and transverse; scuto-scutellar suture absent; prepectus probably fused to mesepisternum but hidden under pronotum; mesepimeron not differentiated from mesepisternum; meso- and metapleura fused but suture distinct; metathorax not distinguishable but apparently transverse (69).

**METASOMA**—"Felt line" developed on second segment, on tergum only, as line of dense pubescence (70). Stridulitrum present as a shield-shaped area on each side at base of fourth tergum (71). First segment somewhat apically constricted, with short petiole; first tergum with lateral margin only very slightly overlying sternum, apparently not movable against sternum although not fused to it except perhaps at basal extreme; first sternum entirely depressed, slightly more so posteriorly, separated from second by a deep constriction (72-76). Second segment not

apically constricted (77). Female with seventh tergum hidden; apex of gonapophysis IX not directed downward (additional details of female terminalia unknown) (78, 81). Male with seventh sternum somewhat reduced although not hidden; hypopygium simple, unmodified; cercus present; gonapophyses IX with notal fusion well-developed (82-87).

LARVA—UNKNOWN.

BEHAVIORAL FORMULA—UNKNOWN.

## 22. *Typhoctid* group.

MATERIAL EXAMINED: *Typhoctes peculiaris* (♂, ♀); *T. striolatus* (♀); *T. williamsi* (♂); *Typhoctoides aphelonyx* (♀). ("Typhoctinae" of the "Mutillidae") (Data also from Reid, 1941; Schuster, 1949; Krombein & Schuster, 1957; Brothers, 1970.)

GENERAL—Sexual dimorphism considerable, male smaller but not much more slender than female; male winged, female apterous (1-2). No sterile caste (3). Much pubescence of sub-plumose setae (4).

HEAD—Clypeus of moderate size; antennae inserted fairly low on face (5). Antennal socket simple, without tubercle (6). Eye oval with inner margin very shallowly sinuate (slightly incised in male), not protuberant; scattered pores with short setae (7-9). Three ocelli present (absent in female) (10). Genal secretory organ absent (11). Antenna with 13 segments in male, 12 segments in female; axis of radicle not deviating much from that of scape; radicle not set into basal invagination of scape (12-14). Labio-maxillary complex not elongated; maxillary palpus 6-segmented; labial palpus 4-segmented (15-17).

MESOSOMA—Pronotum large, very little reduced medially, freely articulating with mesothorax; hind margin arcuate; anterior "collar" well-developed; posterolateral angle rounded, reaching tegula; posteroventral margin approximately straight;

ventral angle rounded, not produced (18-23). Propleura posteriorly contiguous mesally (24). Prosternum sunken except for anterior rim (25). Forecoxae nearly contiguous (26). Mesonotum not much anteriorly produced; scutellum not enlarged (27-28). Prepectus not fused to mesepisternum, discontinuous midventrally, the halves considerably separated, each half very short and tall (29). Mesepimeron reduced, distinguishable only at dorsal extreme (30). Mesosternum simple, without posterior projections (31). Mid-coxae somewhat separated (32). Meso- and metapleura not mutually movable although not fused (33). Metanotum not reduced medially; metapostnotum not visible medially, invaginated (34-35). Metepimeron very slightly expanded anteroventral to endophragmal pit so that pit is a short distance from anterior margin of metapleuron; no metapleural gland (36-37). Metasternum depressed only laterally to accommodate mid-coxae, mesally little differentiated from mesosternum and very slightly anteriorly produced (38-40). Hind coxae contiguous (41). Metathoracic-propodeal pleural suture visible dorsal to endophragmal pit, not distinguishable ventrally (42). Propodeum not shortened; disc and declivity somewhat distinct although merging (43-44). Forewing with venation reduced apically; ten closed cells (45-46). Pterostigma small and sclerotized (47-48). Hind wing with venation reduced apically; three closed cells; veins A and J absent; cu-e originating proximal to separation of M and Cu; free section of Cu present (49-53). Basal hamuli strongly clustered at separation of veins C and SC+R+S (54). Plical lobe not indicated; jugal lobe absent (55-56). Legs slender, generally unmodified; arolia well-developed; claws toothed (57-59). Foretibia with single calcar almost straight, not highly modified (60). Mid-tibia with scattered moderate spines; two simple spurs

(61, 63-65). Hind coxa with weak dorsal carina basally (66). Hind tibia with scattered moderate spines; two simple spurs (62, 64, 67-68). Modified mesosoma of female with pronotum large, articulating with mesothorax; mesonotum extremely short and transverse; scuto-scutellar suture absent; prepectus fused to mesepisternum; mesepimeron not differentiated from mesepisternum; meso- and metapleura fused but suture distinct; metanotum very short and transverse, not distinguishable, fused to propodeum; endophragmal pit barely distinguishable, apparently within meso-metapleural suture; metathoracic-propodeal pleural suture barely visible dorsal to endophragmal pit, not distinguishable ventrally (69).

**METASOMA**—"Felt line" developed on second segment, on tergum only, as line of dense pubescence (70). Stridulitrum present as a shield-shaped area on each side at base of fourth tergum (71). First segment somewhat apically constricted, with short petiole; first tergum with lateral margin only very slightly overlying sternum posteriorly, not movable against sternum although not fused to it except perhaps at extreme base; first sternum entirely depressed, slightly more so posteriorly, separated from second by a deep constriction (72-76). Second segment not apically constricted (77). Female with seventh tergum hidden, reduced but continuously sclerotized anteriorly; no articulation within section 1 of gonocoxite IX; no valve on gonapophysis VIII; gonapophysis IX almost straight with apex weakly directed obliquely upward (78-81). Male with seventh sternum somewhat reduced although not hidden; hypopygium simple, unmodified; cercus present; gonapophyses IX with notal fusion well-developed although slightly desclerotized (82-86).

**LARVA**—Unknown.

**BEHAVIORAL FORMULA**—Unknown.

### 23. *Chyphotid* group.

**MATERIAL EXAMINED:** *Chyphotes attenuatus* (♂); *C. auripilus* (♀); *C. belfragei* (♂, ♀); *C. elevatus* (♂); *C. evansi* (♀); *C. melaniceps* (♂); *C. nubeculus* (♂); *C. petiolatus* (♀); *C. similis* (♂); *Chyphotes* spp. (♂, ♀; Mexico). ("Chyphotini" of the "Mutillidae")

(Data also from Buzicky, 1941; Reid, 1941; Mickel, 1967; Debolt, 1973.)

**GENERAL**—Sexual dimorphism considerable, although male not much more slender than female; male winged, female wingless (1-2). No sterile caste (3). All pubescence simple (4).

**HEAD**—Clypeus of moderate size; antennae inserted fairly low on face (5). Antennal socket with dorsomesal rim produced, forming a moderate tubercle (6). Eye almost round with inner margin sinuate (convex in female), protuberant; scattered pores with short setae (apparently without pores and glabrous in female) (7-9). Three ocelli present (absent in female) (10). Genal secretory organ absent (11). Antenna with 13 segments in male, 12 segments in female; axis of radicle deviating from that of scape at an oblique angle; radicle not set into basal invagination of scape (12-14). Labio-maxillary complex not elongated; maxillary palpus 6-segmented; labial palpus 4-segmented (15-17).

**MESOSOMA**—Pronotum large, not reduced medially (somewhat reduced in male), freely articulating with mesothorax; hind margin almost straight (strongly arcuate in male); anterior "collar" well-developed; posterolateral angle rounded, reaching tegula; posteroventral margin very slightly concave; ventral angle more or less acute, slightly produced (18-23). Propleura posteriorly contiguous mesally (24). Prosternum sunken except for anterior rim (25). Forecoxae nearly contiguous (26). Mesonotum not anteriorly produced (slightly

produced in male); scutellum not enlarged (27-28). Prepectus fused to mesepisternum, discontinuous midventrally, the halves considerably separated, each half very short and tall (29). Mesepimeron reduced, distinguishable only at dorsal extreme (30). Mesosternum simple, without posterior projections (31). Mid-coxae somewhat separated (32). Meso- and metapleura not mutually movable, apparently fused (33). Metanotum not reduced medially; metapostnotum barely visible medially, invaginated (34-35). Metepisternum very slightly expanded anteroventral to endophragmal pit so that pit is a short distance from anterior margin of metapleuron; no metapleural gland (36-37). Metasternum depressed only laterally to accommodate mid-coxae, mesally little differentiated from mesosternum and very slightly anteriorly produced (38-40). Hind coxae contiguous (41). Metathoracic-propodeal pleural suture visible dorsal to endophragmal pit, not distinguishable ventrally (42). Propodeum not shortened; disc and declivity somewhat distinct although merging (43-44). Forewing with venation reduced apically; ten closed cells (45-56). Pterostigma fairly large and sclerotized (47-48). Hind wing with venation reduced apically; two closed cells; vein C reduced distally; veins A and J absent; cu-e originating proximal to separation of M and Cu; free section of Cu present (49-53). Basal hamuli strongly concentrated into a very small basal cluster at separation of vein SC+R+S from margin (54). Plical lobe not indicated; moderate jugal lobe present (55-56). Legs slender, generally unmodified (slightly stouter in female); arolia well-developed (much reduced in female); claws toothed (57-59). Foretibia with single calcar almost straight, not highly modified (60). Mid-tibia with few moderate spines; two simple spurs (spurs dorsally flattened in female) (61, 63-65). Hind coxa appar-

ently simple (with moderate dorsal carina in male) (66). Hind tibia with very few moderate spines apically only; two simple spurs (spurs dorsally flattened in female) (62, 64, 67-68). Modified mesosoma of female with pronotum large, articulating with mesothorax; meso- and metathorax and propodeum entirely fused dorsally and laterally; no sutures visible except that meso-metanotal suture barely evident; mesonotum large, posteriorly expanded; prepectus fused to mesepisternum; propodeum reduced dorsally; disc lost (69).

**METASOMA**—"Felt line" developed on second segment, on tergum only, as line of dense pubescence (70). Stridulitrum present as a shield-shaped area on each side at base of fourth tergum (71). First segment somewhat apically constricted, with marked petiole; first tergum with lateral margin only very slightly overlying sternum posteriorly, not movable against sternum and fused to it basally, much narrowed along petiole (tergum apparently absent from petiole in female); first sternum depressed, slightly more so posteriorly, separated from second by a deep constriction (72-76). Second segment not apically constricted (77). Female with seventh tergum hidden, reduced but continuously sclerotized anteriorly; no articulation within section I of gonocoxite IX; no valve on gonapophysis VIII; gonapophysis IX almost straight, with apex weakly directed obliquely upward (78-81). Male with seventh sternum somewhat reduced, not entirely hidden; hypopygium basally concealed by sixth and seventh sterna, apically produced as three spines, the middle one produced and upcurved; cercus present; gonapophyses IX with notal fusion extensive (82-86).

**LARVA**—Unknown.

**BEHAVIORAL FORMULA**—Unknown.

#### 24. *Apterogynid* group.

**MATERIAL EXAMINED:** *Apterogyna algirica*

(♂); *A. aliwalica* (♀); *A. bembesia* (♀); *A. bimaculata* (♀); *A. bulawayona* (♂); *A. geyri* (♂); *A. globularis* (♂); *A. guillarmodi* (♀); *A. karroa* (♂); *A. kochi* (♂); *A. olivieri* (♂, ♀); *A. patrizii* (♂); *A. savignyi* (♂, ♀); *A. schultzei* (♂, ♀); *A. villiersi* (♂). ("Apterogynini" of the "Mutillidae")

(Data also from Reid, 1941; Giner Marí, 1944; Invrea, 1957.)

GENERAL—Sexual dimorphism considerable, although male not more slender than female; male winged, female apterous (1-2). No sterile caste (3). All pubescence simple (4).

HEAD—Clypeus of moderate size; antennae inserted fairly low on face (somewhat higher in male) (5). Antennal socket with dorsomesal rim produced, forming well-developed tubercle (6). Eye oval, somewhat shortened and almost round, with inner margin extremely shallowly sinuate (convex in female), protuberant; pores and setae apparently absent (7-9). Three ocelli present (absent in female) (10). Genal secretory organ well-developed (11). Antenna with 13 segments in male, 12 segments in female; axis of radicle deviating from that of scape at an oblique angle; radicle not set into basal invagination of scape (12-14). Labio-maxillary complex not elongated; maxillary palpus 6-segmented; labial palpus 4-segmented (15-17).

MESOSOMA—Pronotum large, not reduced medially (much reduced in male), freely articulating with mesothorax; hind margin shallowly arcuate (deeply concave in male); anterior "collar" well-developed; posterolateral angle rounded, reaching tegula; posteroventral margin very slightly concave; ventral angle acute, slightly mesally produced (18-23). Propleura posteriorly contiguous mesally (24). Prosternum sunken except for anterior rim (25). Forecoxae contiguous (26). Mesonotum not anteriorly produced (considerably pro-

duced in male); scutellum somewhat enlarged and swollen posterodorsally (27-28). Prepectus not fused to mesepisternum, discontinuous midventrally, the halves considerably separated, each half extremely short and tall (29). Mesepimeron reduced, distinguishable only at dorsal extreme (30). Mesosternum simple, without posterior projections (31). Mid-coxae somewhat separated (considerably separated in female) (32). Meso- and metapleura not mutually movable although apparently not fused (33). Metanotum somewhat reduced medially; metapostnotum not visible medially, invaginated (34-35). Metepisternum expanded anterior to endophragmal pit so that pit is some distance from anterior margin of metapleuron; no metapleural gland (36-37). Metasternum depressed only laterally to accommodate mid-coxae, mesally little-differentiated from mesosternum and considerably anteriorly produced (38-40). Hind coxae contiguous (41). Metathoracic-propodeal pleural suture visible dorsal to endophragmal pit, not distinguishable ventrally (42). Propodeum slightly shortened dorsally; disc and declivity somewhat distinct although merging (43-44). Forewing with venation much reduced apically; five closed cells; cells R, 1S, 2S, S+M, 1M absent (45-46). Pterostigma very small and sclerotized (47-48). Hind wing with venation considerably reduced apically; three closed cells; veins A and J absent; cu-e originating proximal to separation of M and Cu; free section of Cu present (49-53). Basal hamuli absent (54). Plical lobe not indicated; moderate jugal lobe present (55-56). Legs slender, generally unmodified (slightly stouter in female); arolia much reduced; claws toothed (57-59). Foretibia with single calcar considerably curved and flattened with an outer spine apically (60). Mid-tibia with very few moderate spines apically only; two spurs flattened and with



strongly toothed margins (61, 63-65). Hind coxa with moderate dorsal carina (66). Hind tibia with very few moderate spines apically only; two spurs flattened and with strongly toothed margins (62, 64, 67-68). Modified mesosoma of female with pronotum large, articulating with mesothorax; meso- and metathorax and propodeum entirely fused dorsally and laterally; meso-metanotal suture barely evident; mesonotum large, somewhat posteriorly expanded; prepectus fused to mesepisternum; meso- and metapleura fused but suture visible; line of fusion between nota and pleura of meso- and metathorax weakly marked; metathoracic-propodeal suture entirely obliterated; propodeum reduced dorsally; disc lost (69).

**METASOMA**—"Felt line" developed on second segment, on tergum only, as line of dense pubescence (as invaginated cuticular line in female) (70). Stridulitrum absent (71). First segment considerably constricted apically, nodose, with marked petiole; first tergum with lateral margin only very slightly overlying sternum posteriorly, not movable against sternum and fused to it basally, much narrowed along petiole; first sternum depressed, slightly more so posteriorly, separated from the second by a deep constriction (72-76). Second segment considerably constricted apically (77). Female with seventh tergum hidden, reduced but continuously sclerotized anteriorly; no articulation within section 1 of gonocoxite IX; valve present on gonapophysis VIII; gonapophysis IX almost straight with apex weakly directed obliquely downward (78-81). Male with seventh sternum reduced but not entirely hidden; hypopygium not concealed basally, apically produced as three spines, the middle one produced and up-curved; cercus absent; gonapophyses IX with notal fusion extensive (82-86).

**LARVA**—Unknown.

**BEHAVIORAL FORMULA**—Unknown.

### 25. *Bradynobaenid* group.

**MATERIAL EXAMINED:** *Bradynobaenus australis* (♂); *B. gayi* (♂, ♀); *B. wagenknechti* (♂); *Bradynobaenus* spp. (♀ ♀); Chile, Argentina). ("Bradynobaeninae" of the "Tiphiiidae")

(Data also from Spinola, 1851; Zavattari, 1910; Reid, 1941; Pate, 1947a; Pérez D'Angello, 1968.)

**GENERAL**—Sexual dimorphism considerable although male not more slender than female; male winged, female apterous (1-2). No sterile caste (3). All pubescence simple (4).

**HEAD**—Clypeus of moderate size; antennae inserted fairly low on face (5). Antennal socket with dorsomesal rim very slightly produced but no true tubercle; interantennal frons slightly produced and forming a weak frontal ledge (6). Eye broadly oval with inner margin extremely shallowly sinuate, not protuberant; pores and setae apparently absent (7-9). Three ocelli present (10). Genal secretory organ present (not clearly distinguishable in male) (11). Antenna with 13 segments in male, 12 segments in female; axis of radicle deviating from that of scape at an oblique angle; radicle not set into basal invagination of scape (12-14). Labio-maxillary complex reduced; maxillary palpus 2-segmented; labial palpus 3-segmented (15-17).

**MESOSOMA**—Pronotum large, not reduced medially (extremely reduced in male), freely articulating with mesothorax; hind margin shallowly arcuate (very deeply concave in male); anterior "collar" moderate; posterolateral angle rounded, reaching tegula, slightly posteriorly produced below tegula; posteroventral margin slightly concave; ventral angle acute, slightly mesally produced (18-23). Propleura posteri-

orly contiguous mesally (24). Prosternum sunken except for small anterior rim (25). Forecoxae nearly contiguous (26). Mesonotum not anteriorly produced (greatly produced in male); scutellum much enlarged and swollen posterodorsally, overhanging metanotum (27-28). Prepectus not fused to mesepisternum, discontinuous midventrally, the halves considerably separated, each half extremely short and tall (29). Mesepimeron reduced, distinguishable only at dorsal extreme (30). Mesosternum simple, without posterior projections (31). Mid-coxae somewhat separated (considerably so in female) (32). Meso- and metapleura not mutually movable although apparently not fused (33). Metanotum somewhat reduced medially; metapostnotum not visible medially, invaginated (34-35). Metepisternum expanded anterior to endophragmal pit so that pit is some distance from anterior margin of metapleuron but sutures anterior to pit are indistinct; no metapleural gland (36-37). Metasternum depressed only laterally to accommodate mid-coxae, mesally little differentiated from mesosternum and considerably anteriorly produced (moderately produced in female) (38-40). Hind coxae contiguous (41). Metathoracic-propodeal pleural suture visible dorsal to endophragmal pit, very indistinctly distinguishable ventrally (42). Propodeum considerably shortened dorsally; disc virtually non-existent, distinct from declivity (43-44). Forewing with venation extremely reduced apically; three closed cells; cells R, SC+R, 1S, 2S, S+M, 1M, 1Cu absent (45-46). Pterostigma very small and sclerotized (47-48). Hind wing with venation extremely reduced apically; two closed cells; vein M+Cu absent; veins A and J absent; cu-e originating proximal to separation of M and Cu; free section of Cu present (49-53). Basal hamuli absent (54). Plical lobe not indicated; moderate jugal lobe present (55-56). Legs fairly

slender, little modified (considerably stouter in female); arolia much reduced; claws simple (57-59). Foretibia with single calcar considerably curved and flattened with an outer spine apically (spine absent in female) (60). Mid-tibia with few strong spines apically only; no spurs (61, 63-65). Hind coxa simple (66). Hind tibia with few strong spines apically only; two spurs flattened with a few teeth on margins (nematiform and smooth in female) (62, 64, 67-68). Modified mesosoma of female with pronotum large, articulating with mesothorax; meso- and metathorax and propodeum entirely fused dorsally and laterally; meso-metanotal suture barely evident; mesonotum large, somewhat posteriorly expanded; prepectus fused to mesepisternum; meso-metapleural suture faintly visible; line of fusion between nota and pleura of meso- and metathorax distinct; metathoracic-propodeal suture entirely obliterated; propodeum reduced dorsally; disc lost (69).

**METASOMA**—"Felt line" developed on second segment, on tergum only, as invaginated cuticular line in both sexes (70). Stridulitrum absent (71). First segment slightly constricted apically, with short petiole; first tergum with lateral margin only very slightly overlying sternum posteriorly, not movable against sternum and fused to it basally, much narrowed along petiole; first sternum depressed, more so posteriorly, separated from second by a deep constriction (72-76). Second segment not apically constricted (77). Female with seventh tergum hidden, reduced but continuously sclerotized anteriorly; no articulation within section 1 of gonocoxite IX; no valve on gonapophysis VIII; gonapophysis IX strongly curved, especially basally, with apex downwardly directed (78-81). Male with seventh sternum reduced but not entirely hidden; hypopygium not concealed basally, apically produced as three subequal spines; cercus absent;

gonapophyses IX with notal fusion extensive (82-86).

LARVA—Unknown.

BEHAVIORAL FORMULA—Unknown.

## Discussion

### CLADISTIC RELATIONSHIPS

Surprisingly, there have apparently been few intensive attempts to derive a phylogeny of the aculeate Hymenoptera. Although various schemes have been proposed (e.g., Ashmead, 1896b; Börner, 1919; Evans, 1958, 1966b; Ross, 1965; Evans & West Eberhard, 1970), these generally do not explicitly state the data on which they are based, or else they are based on a very limited data set so that detailed comparisons with the present scheme are of little value. A recent scheme of the evolution of the Hymenoptera is that of Evans & West Eberhard (1970), the upper section of which is shown in Fig. 62. This diagram expresses the commonly accepted ideas on aculeate evolution and should be used as the frame of reference for discussion of the present scheme (Fig. 2).

Basically, a sequence of more or less straight-line evolutionary advancement seems to have been emphasized, so that the more "primitive" groups (e.g., bethyloids and scolioidea) are shown as arising early and the more "advanced" groups (e.g., apoidea) are derived at the apex of the tree (Fig. 62). It now seems that some of the most "advanced" groups originated near the base of the tree and subsequently diverged greatly from the original stock. (This in essence reemphasizes the inappropriateness of the terms "primitive" and "advanced" as applied to entire taxa.) It is of some interest that Spradbery (1973) has recently presented a diagram which is somewhat more similar to that derived here in that he shows the line leading to the bees arising above the bethyloids but

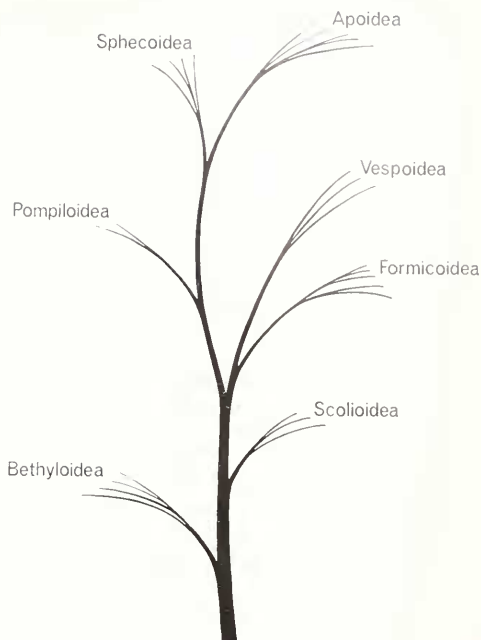


FIG. 62. Phylogeny of the traditional superfamilies of Aculeata, according to Evans & West Eberhard (1970).

below the scolioidea. On the other hand, he places the chrysidids in the Terebrantia, which is at variance with most other schemes.

In the present cladogram the scolebythids are extremely close to the bethylid group and may even have been derived from a stock very similar to modern "Bethylidae," indicating that this group is clearly more strongly associated with the bethylid group than any other. (Evans, 1963, by contrast, included the scolebythids in the "Scolioidea.") Although the plumariids possess many characters in states which have otherwise occurred only in lines on or above internode 1-4, they are linked to the bethylids and scolebythids by the common development of an articulation within section 1 of gonocoxite IX in the female and by the loss of the jugal lobe in the hind wing.

The remaining aculeates are strongly associated, most strikingly by common possession of sexual dimorphism in the num-

ber of antennal segments (13 segments in male and 12 segments in female), and reduction and desclerotization of the seventh metasomal tergum in the female. Thus the basal division of the Aculeata into two holophyletic lines as proposed by Oeser (1961) is not contradicted here.

The common ancestor of the sphecid and apid lines apparently diverged very early from the other aculeates, thus establishing a separate and highly divergent line. This is most strikingly characterized by the forms of the pronotum, metapostnotum and metapleuron, which serve to associate the apid and sphecid groups very strongly.

The remaining line of aculeates is not associated by any very strong character states, although the posterior approximation of the propleura, shortening of the prepectus, anterior depression of the metasternum, loss of veins A and J (hind wing) and deepening of the axillary incision may all have occurred on a line (internode 4-6) associating this group. These character states have also evolved elsewhere, however, although the first and second are probably the strongest and appear on the cladogram only once each.

Within this grouping there appear to be two lines, one of which is much more firmly established than the other. The group containing the tiphids, mutillids and their relatives (subtended by internode 6-7) is associated by a number of reasonably good character states, such as the distal position of crossvein cu-e (hind wing), the partial invagination of the metapostnotum and the reduction of the second larval spiracle (which has apparently been reversed in, or within, the sapygids). Although these are individually not particularly impressive, the entire complex of character states involved is evidently significant. Within this group the association of the sapygids, myrmosids and mutillids is based on some quite strong

character states, especially the loss of the free section of vein Cu (hind wing) (although with apparent reversal within the mutillid group), reduction of the jugal lobe of the hind wing, and desclerotization and basal retraction of the gonapophyseal notum in the male. Although the myrmosids have recently commonly been included in the "Tiphidae" (e.g., Krombein, 1940; Pate, 1947a), their association with the mutillids appears much stronger, being based particularly on the form of the scape, fusion of the prepectus to the mesepisternum, the form of the modified female mesosoma, and the mesal stridulitrum. The general similarity between the myrmosids (males) and *Fedtschenkia* (sapygid group) is also quite marked, especially in wing venation, reinforcing the grouping of these taxa. It is of some interest that *Fedtschenkia* was first described as a member of the Mutillidae (Saussure, 1880) and a short time later was placed in a separate tribe of the mutillids since "ils forment le trait d'union entre les Mutillines et les Sapygides" (Saussure, 1892). If indeed *Fedtschenkia* is correctly considered to be a relatively "primitive" member of the "Sapygidae" (a placement that was not found to be contradicted during the present study), then the present investigation supports this relationship which was first suggested more than 80 years ago. (Guiglia, 1955, 1969, has outlined the taxonomic history of *Fedtschenkia*.)

The group containing the tiphids consists of six taxa associated (on internode 7-10) by rather few characters of which the major one is probably the development of lamellate projections over the mid-coxae (although these have been reduced in the methochids). The group is also associated by a somewhat similar body form, especially of the females. The five taxa beyond the anthoboscids share a tendency towards reduction or loss of the wings in the fe-

male, resulting in similar mesosomal modifications, although the tiphid group does not exhibit complete aptery in any member. The four taxa beyond the thynnids are strongly associated by the modification of the male hypopygium as a simple up-curved aculeus. The myzinid and methochid groups share males of a peculiar elongate form, in particular, and the tiphids and brachycistids both have the seventh sternum and hypopygium of the male almost completely concealed, amongst other shared character states.

The remaining taxa (subtended by internode 6-15) are very weakly associated basally and may not represent a holophyletic group. Internodes 6-15, 15-16 and 16-18 are all rather weak (each bearing relatively few character states, most of which occur numerous times elsewhere on the cladogram) and may not be supported when additional data are considered. Despite these limitations, the sierolomorphids do appear to be similar to the pompilid group and also the typhoctids, especially in the structure of the female genitalia. The pompilids and rhopalosomatids are quite strongly associated, particularly by the similar development of a calcar on the hind tibia, and to some extent by the venation of the hind wing (especially the loss of the apical section of vein E).

The ten taxa above the sierolomorphids are associated (on internode 15-16) by the clustering of the basal hamuli, the reduction in the size of the pterostigma and perhaps the reduction in the number of teeth on the larval mandible (tridentate or less), all rather weak characters, especially the last since the larva is unknown for the entire branch subtended by internode 18-21. Association of the eight apical groups (above internode 16-18) is mainly on the basis of the complete invagination of the metapostnotum, which has also occurred elsewhere.

The formicid-vespid-scoliid line is as-

sociated by the common production of the ventral angle of the pronotum and anterior expansion of the metepisternum and metepimeron (which is least obvious in the scoliids). These are probably not very strong character states. However, the formicid and vespidae groups share other states, such as the extreme reduction of the prepectus, the use of numerous prey individuals and early oviposition, which may additionally indicate some association based on parallel development of these character states. By contrast, the somewhat unexpected association of the scoliids and vespidae seems to be based on a number of good character states. These include especially the form of the pronotum and its close association with the mesothorax, as well as the reniform eyes, dorsally produced clypeus, sunken prosternum and membranous pterostigma. (They of course also share all derived states appearing on internodes below internode 19-20.) Both of these taxa also possess highly muscular and similarly modified venom reservoirs with the muscle strands running transversely (Robertson, 1968), which supports this relationship, although Robertson came to somewhat different conclusions in her study which was based on a rather limited data set.

The remaining five taxa are very strongly associated (on internode 18-21) by a number of characters, such as the form of the metasternum, the basic form of the modified mesosoma in females (all of which are apterous), the presence of dorsal "felt lines" and the paired stridulitra (which are, however, lost in the apterogynids and bradynobaenids). Within this group the eotillids and typhoctids are strongly linked by the form of the mesosoma in the female. The other three taxa share an angulate scape, a similarly modified mesosoma in the female, a similarly modified first metasomal segment, and a trispinose hypopygium in the male. The

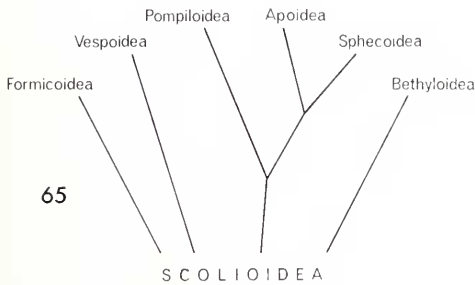
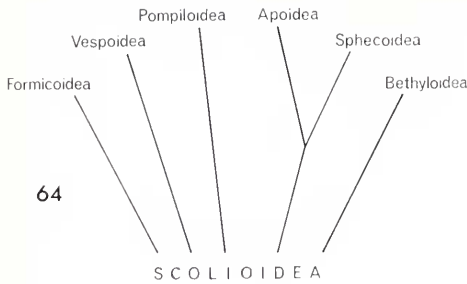
association of the apterogynids and bradynobaenids has been mentioned previously by Reid (1941) and in passing by Bischoff (1927); it is strongly supported, particularly by the specialized genal organ, the enlarged scutellum, the identical modification of wing venation and the form of the foretibial calcar.

When life history data are considered, the cladogram does not contradict the idea that the ancestral aculeates were associated with hemimetabolous insects, such as Orthoptera or Hemiptera, which may have been more plentiful than the more recently evolved holometabolous groups. Thus, for example, various members of the bethylid group attack Hemimetabola [dryinids and embolemids on Homoptera (Ponomarenko, 1972; Evans, 1964a), mesitiines on Orthoptera (Gryllidae) (Nielsen, 1932)—although Nagy, 1969c, found *Mesitius horvathi* parasitic on a clythrine beetle—and sclerogibbids on Embioptera (Callan, 1939; Richards, 1939)], as do the most generalized sphecoids [ampulicids on Blattodea and sphecines mainly on Orthoptera (Clausen, 1940)], these taxa representing the most basal groups on the cladogram. Within each of these taxa there have been departures to the use of Holometabola [e.g., Coleoptera larvae by many "Bethylidae" (Evans, 1964a), Diptera and Lepidoptera by higher "Nyssoninae" (Evans, 1966a)]. The rhopalosomatids attack Orthoptera (Gryllidae) (Gurney, 1953) and the pompilids utilize spiders (Evans, 1953), another ancient group. Above internode 4-5, the apids have undergone a drastic change to the use of pollen and nectar (Malyshev, 1968). On internode 7-8 a change to parasitization of other Hymenoptera nesting in the soil apparently occurred. This is the basic habit of the sapygid (Bohart & Schuster, 1972), myrmosid and mutillid (Mickel, 1928) groups, although many sapygids have become cleptoparasitic on bees

(Malyshev, 1968; Torchio, 1972) and a few mutillids parasitize hosts other than Hymenoptera (Brothers, 1972). All the taxa above internode 7-10 utilize cryptic coleopterous larvae (Pate, 1947a), as do the scoliids (Clausen, 1940) (this probably resulting in the convergence of body form between various tiphioids and the scoliids). (The hosts are actually unknown for the brachycistidid group, but see Wasbauer, 1966.) Primitive formicids have adopted a predatory habit connected with their sociality (Wilson, 1971). The vespids use many prey individuals of various types with which they provision their complex nests, and a large group of these (the masarids) has adopted pollen and nectar (although some of the most primitive masarids—*Euparagia*—use the larvae of weevils; Williams, 1927). Unfortunately, nothing is known of the life histories of plumariids, scolebythids (although parasitism of woodboring beetle larvae is probable; Evans, 1963), sierolomorphids, typhoctids, cotillids, chyphotids, apterogynids or bradynobaenids, so that they cannot be related to this scheme.

Although such attempts can be made to correlate prey or host group with a cladogram derived almost entirely from morphological characters, much more work is needed on the life histories of most groups of Aculeata before any more definite indications of the patterns of evolution of host relationships can be given. Data on entirely new aspects of behavior will also undoubtedly prove useful. For example, Farish (1972) examined grooming behavior in 51 species of aculeates (as well as other Hymenoptera) and applied the results to a somewhat unusual phylogeny which he had constructed from previously published information. Although very incomplete (due to poor representation in some groups), the patterns derived seem to confirm the distinctness of the Aculeata. Again, additional investigations





FIGS. 64-65. Relationships of the traditional superfamilies of Aculeata. 64, from the present study, considering the ancestral aculeate to be a member of the Scolioidea; 65, according to Evans (1958).

rived characters present on internode 1-4, it is not appropriate to consider the ancestor below node 1 to be a member of the "Scolioidea," so that this scheme is also inadequate. It is also singularly lacking in information content.

The "Pompiloidea" has commonly been considered as derived from the line leading to the sphecoids and apooids, apparently because the posterolateral angle of the pronotum is rather rounded in the pompilids, a condition which has been regarded as a precursor to that in the sphecoids and apooids. Actually the primitive condition in the pompilids is not unlike that in many of the more generalized scolioids, such as *Anthobosca* or *Sierolomorpha*, although the lobe over the spiracle is somewhat emphasized by the presence of a dorsoventral groove in the pompilids. Furthermore, the pompilids do not possess any of the other unique modi-

fications, such as the form of the metapostnotum and metapleuron, which are characteristic of the apooids and sphecoids. It is thus clear that there is no good character to link the pompilids to the sphecoid-apoid line. Instead, the pompilids show more affinities with the formicoid-vespoid line.

#### DERIVATION OF A CLASSIFICATION

Given the present cladogram (Fig. 2), the question arises as how best to translate it into a classificatory scheme and whether the traditional superfamilies ("Bethyloidea," "Scolioidea," "Pompiloidea," "Vespoidea," "Formicoidea," "Sphecoidea" and "Apoidea") should logically continue to be recognized as such. The basic branching pattern (the result of cladogenesis) is only one aspect to be considered; degree of relative morphological or phenetic distinctness of taxa (the result of anagenesis) is another. The latter is difficult to measure objectively in such a way that it can be incorporated directly into a cladogram.

A simple method of estimating phenetic divergence might merely involve summing the number of derived character states on each particular internode, thus deriving an index of phenetic divergence for that internode. (For any taxon in which the state of a character is unknown, the primitive state is assumed unless otherwise indicated by the distribution of derived states in related taxa.) This is not sufficient, however, since degree of classificatory (or taxonomic) distinctness is somewhat dependent on the sizes of the groups involved, as is expressed in Mayr's (1969:92) recommendation that, for taxa above the species level, "the size of the [phenetic] gap [separating a taxon from another of the same categorical level] be in inverse ratio to the size of the taxon." This is purely a formalistic requirement designed to facilitate the data retrieval or



reference functions of a classification by minimizing the proliferation of named taxa each containing only one or a few rather distinctive species. It has further been suggested by Ashlock (pers. comm.) that it may be logical to judge the relative importance of the various internodes in terms of the "success" of the groups derived from those internodes, possibly by considering the number of species in each group. Although "success" undoubtedly involves many other factors, most of these, such as biomass, number of individuals or energy flow, are incapable of adequate quantification in practice. (See Van Valen, 1973, for a discussion of criteria for comparison of taxa at the same categorical level in different phyla.)

The importance ("distinctness") of a particular internode may thus be estimated by devising some index that combines the number of evolutionary innovations (most conveniently represented as hatch marks) on that internode and the number of species that has been produced by the various lines derived from it. A simple product of these numbers appears to serve this purpose, as has been suggested by Ashlock (pers. comm.). Such a distinctness measure based on numbers or frequencies ( $df$ ) may be expressed as

$$df_m = k_m S_m \quad (1)$$

where  $k_m$  equals the number of derived character states (hatch marks) on internode (or final branch)  $m$  (assuming each such state to appear once on the branch) and  $S_m$  equals the total number of species subtended by internode  $m$ .

There is, however, an additional factor to consider: the fact that the distinctness of a group depends on the uniqueness of the derived character states delimiting the group. Thus a group characterized by the possession of many states uniquely derived (i.e., possessed by that group only) may logically be regarded as more distinct than

one which possesses an equal number of states which have been derived more than once on the tree. The weight to be attached to any derived character state in assessing its significance as a delimiter of taxa for any internode, may logically be considered to be proportional to the ratio of its frequency of occurrence on that internode (assumed as unity) to its total frequency on the entire tree. This value is the reciprocal of the total number of times that it appears on the tree. Based on these considerations, another measure of distinctness for each internode (and final branch) utilizes the reciprocal of the harmonic mean (i.e., the mean of the reciprocals) of the number of times that each derived character state falling on that internode appears on the entire tree. (Although some character states appear only once on the tree, they may have been derived within other groups elsewhere on the tree. Such states are obviously not as efficient in delimiting groups as are those which appear only once on the tree and have not been derived elsewhere. It is impossible to differentiate between these two types in practice when dealing with very large groups, however, so that only occurrences shown on the tree can be included.) Maximal distinctness of a branch (all character states uniquely derived) is given by a value of 1, with decreased distinctness being less than 1 but greater than 0 (unless the internode bears no derived states). This distinctness measure based on character state efficiencies ( $de$ ) may be expressed as

$$de_m = \frac{\left( \sum_{j=1}^k N_j^{-1} \right)_m}{k_m} \quad (2)$$

where  $N_j$  equals the total number of times that derived character state  $j$  appears on the entire cladogram and  $k_m$  (as before) equals the number of derived character

states (hatch marks) on internode (or final branch)  $m$  (assuming each such state to appear once on the branch). This index is identical to the mean of the "unit character consistencies" (Farris, 1969) for the "characters" on the internode if each character state is considered as a separate "character" (i.e., each has a range of one unit).

Neither of these measures alone is sufficient to provide an adequate idea of distinctness; since all the factors mentioned must be taken into account, a combination should be more useful. This is easily derived as the product of  $df$  and  $de$ . Thus, a more complete measure of distinctness ( $dc$ ) for any internode or final branch  $m$  may be given as

$$dc_m = df_m de_m = S_m \left( \sum_{j=1}^k N_j^{-1} \right)_m \quad (3)$$

Once such a measure of distinctness has been obtained for each branch, it is a simple matter to construct a matrix presenting the taxonomic distinctness ( $dt$ ) of each taxon from every other taxon. This is done by summing the distinctness values for each branch linking the two taxa ( $X$  and  $Y$ ) under consideration. This may be expressed as

$$\begin{aligned} dt_{X,Y} &= \sum_{m=1}^p dc_m \\ &= \sum_{m=1}^p \left[ S_m \left( \sum_{j=1}^k N_j^{-1} \right)_m \right] \quad (4) \end{aligned}$$

where  $p$  is the number of internodes and final branches between taxon  $X$  and taxon  $Y$  including the most recent common ancestor of  $X$  and  $Y$ , and the other symbols have the same meaning as before. These final figures are essentially weighted measures of total "patristic difference" (Farris, 1967) or "number of steps" in the sense of Camin & Sokal (1965). They may be used in judging appropriate levels of distinctness for allocating the various

taxa to different categorical levels (such as genus, family, etc.) in the final classification.

There is a complication introduced into the present study as a result of differential evolution of the two sexes. In some instances a particular derived state is present in one sex only although it could potentially occur in both. Such a derived state is obviously not as effective in distinguishing between taxa as is one which does not exhibit such dimorphic development, and thus should not be given equal weight in the calculation of a distinctness measure. (This of course does not deny that such a character state may be equally valid in a cladistic sense as a reflection of significant genetic modification as is one which occurs in both sexes.) For states appearing on the tree at least once in both sexes, it thus seems logical to score each occurrence of the state in one sex only as 0.5, and when affecting both sexes as 1.0. Character states occurring on the tree in only one sex or logically applicable to one sex only (such as those of the female genitalia) should also be coded as 1.0 since there is no *a priori* reason to consider these less significant than those appearing in both sexes.

These adjustments (or any other type of weighting to take similar factors into account) invalidate the assumptions made earlier that each state appearing on an internode appears there once. The previously derived equations (1-4) must thus be made more general. When this is done it becomes obvious that  $k_m$  in equation 2 is not the same factor as that symbolized by  $k_m$  in equation 1. The generalization follows:

Assume no limitation on the number of occurrences of each derived character state  $j$  on any internode  $m$ . Now,

$$DF_m = \left( \sum_{j=1}^k i_j \right)_m S_m \quad (5)$$

where  $i_j$  is the number of occurrences  $i$  of each derived state  $j$ , and  $k$  is the number of derived states, both on internode (or final branch)  $m$ ; and  $S_m$  equals the total number of species subtended by internode  $m$ , as before.

Since unitary occurrence of each derived state on any one internode is now not assumed, the measure of distinctness based on efficiencies can no longer be based directly on the harmonic mean of the number of times each state appears on the entire tree. Instead, the "efficiency" of each state  $j$  is directly calculated as the ratio of the frequency of its occurrence on the internode to its frequency on the entire cladogram, and the mean of these ratios for all  $k$  states is then utilized. The limits of 0 and 1 still hold, as long as no state is considered to occur less than once in the entire tree. Thus,

$$DE_m = \frac{\left[ \sum_{j=1}^k \left( \frac{i_{j_m}}{\sum_{m=1}^n i_{j_m}} \right) \right]_j}{k_m} \quad (6)$$

where  $i_{j_m}$  is the number of occurrences of derived character state  $j$  on internode (or final branch)  $m$ ,  $k_m$  is the number of derived character states (hatch marks) on internode  $m$  (as before), and  $n$  is the number of internodes (and final branches) in the cladogram.

There is no longer any cancellation of terms in the formula when the product of  $DF$  and  $DE$  is found, so that  $DC$  cannot be calculated directly. Now,

$$DC_m = DF_m DE_m \quad (7)$$

The taxonomic distinctness of any two taxa,  $X$  and  $Y$ , is thus measured as

$$DT_{XY} = \sum_{m=1}^p DC_m \quad (8)$$

where  $p$  is the number of internodes and

final branches between taxon  $X$  and taxon  $Y$ , including the most recent common ancestor of  $X$  and  $Y$ .

These generalized equations (5-8) are those used in the present study. For investigations where the assumption of one occurrence on any internode for each derived state is valid, the earlier equations (1-4) are easier to apply, especially since  $DC$  can then be calculated directly.

A word is necessary to clarify the method of determining the number of occurrences of a character state. There are two aspects which may cause confusion. First, a particular derived state is sometimes apparently reversed to the primitive or a less derived condition. Since the original primitive state cannot be placed on any internode, the only appearances of the "primitive" state will be the result of such reversals. As such, it seems most appropriate to consider these as "pseudo-primitive" states and treat them like any other derived state, merely totalling the number of times that each appears on the tree. On the other hand, a reversal to an already derived state (e.g., from state C.2.1 to C.2) represents another appearance of a state which is already placed elsewhere on the tree. Although this actually represents a further derivation (in the above example it might be numbered C.2.1.1) in a cladistic sense, it nevertheless is equivalent to the less-derived state (C.2) in a phenetic sense, and so should be counted among the occurrences of that less-derived state. The second problem concerns instances in which a highly derived state apparently arises *de novo*, there being no evidence of an intermediate state which is found elsewhere on the tree (e.g., state C.3.1.1 is derived directly from C.3 although elsewhere on the tree it is derived from C.3.1). The usual practice in constructing the cladogram is to enter the missing intermediate state on the internode with its logical derivative. If there

is absolute certainty that such an intermediate is required for that subsequent derivation to be possible, then this placement of states is justified. Such certainty is usually not possible, however, since a similar highly derived state may often logically have arisen in different ways from different intermediates. Some of these intermediates may not be present in the material examined, so that they do not appear in the coding of character states. Thus, inferring the occurrence of a particular derived state on an internode merely because of the presence of a state which may logically be derived from it, is probably unwarranted in most instances. Such inferred derivations should thus not usually be included when counting the occurrences of a particular state.

It should be emphasized at this point that the measures of taxonomic distinctness ( $DT$ ) should not be considered to provide absolute criteria or definite numerical values at which groups are automatically considered distinct at some pre-determined taxonomic level. (As Sneath & Sokal, 1973, emphasize, groups delimited in an analogous fashion on phenograms by means of phenon lines "approach natural taxa more or less closely" but are more appropriately termed "phenons" and are not allocated levels in the formal taxonomic hierarchy.) Instead, these measures may be used as indices from which some indication of the size of the phenetic gap between two groups, as well as the relative variation within a cluster of groups, may be gauged. As is indicated by Sneath & Sokal (1973), the most important criteria on which to base decisions on taxonomic rank are probably the internal diversity of a taxon and the sizes of the gaps between a taxon and those adjacent to it. Despite the significance generally attached to the "gap criterion" by practicing taxonomists of the "evolutionary" school (Michener, 1970), it is re-

jected by Sneath & Sokal (mainly because a gap is almost incapable of being measured using the usual numerical phenetic techniques). The distinctness measures derived above seem to be interpretable in terms of both criteria, however.

Because of the branching structure of a cladogram, involving hierarchical levels of dichotomy, use of the absolute number of species for calculation of  $DF$  is not appropriate. Instead, a multiplicative (logarithmic or exponential) conversion

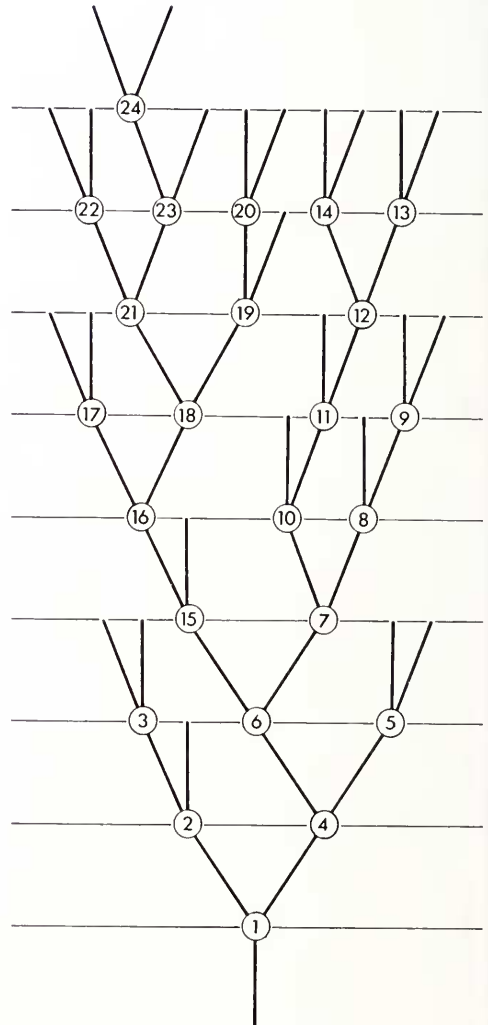


FIG. 66. Cladogram of 25 taxa of Aculeata, as in Fig. 2, emphasizing the number of levels of dichotomy.

scale should be used. It may be proposed that the logarithm to the base 2 is appropriate since this represents the number of levels of dichotomy in a perfectly regular tree which gives rise to the number of end points (species) involved. Cladograms are practically never perfectly regular, however. If one were able to count the number of levels involved in an actual cladogram, the number would almost invariably be greater than for a perfectly regular branching pattern involving the same number of species. For example, the present cladogram of the Aculeata (with 25 final branches) may be considered to involve 9 levels of dichotomy (see Fig. 66 for derivation) although a perfectly regular dendrogram with the same number of final taxa would have about half that number of levels ( $4 < \log_2 25 < 5$ ). A scale based on consideration of the number of levels of dichotomy is thus not logically required. Furthermore, a logarithmic scale has the effect of drastically reducing the weight of a very large group in comparison with the small ones. This effect is not as extreme if an exponential scale is used. In the present study some groups were extremely large, and the cube root of the estimated number of species in each group was thus used for the values of  $S_m$ . (The number of species in each group is a best estimate based on the information contained in a wide variety of papers cited elsewhere in this account.)

Values of  $\Sigma i$ ,  $k$ ,  $S$ ,  $DF$ ,  $DE$  and  $DC$  for the Aculeata appear in Table I, and those of  $DT$  are shown in Table II. The taxa are arranged from the base of the tree to the apex, taking each branch in turn.

The taxonomic distinctness measures ( $DT$ ) for the Aculeata range from 5 to 1048 (mean 454). In general, the long diagonal in Table II contains the values between the closest pairs on the tree except where different branches are involved.

These values are all below the mean for the study, except for two. These are the values between the plumariids and sphecids (566) and between the apids and anthoboscids (713). Furthermore, the values between all the basal taxa on the branches represented by these taxa (considering in addition sphecids to sierolomorphids, 489) are greater than the mean. This suggests a fundamental division into three groups, these subtended by internodes 1-2, 4-5, and 4-6 respectively.

Within the first of these groups (containing plumariids, bethylids and scolebythids) the values of  $DT$  are all quite low (mean is 77) although that between the scolebythids and bethylids is much lower than the others. This indicates relatively slight internal variation within this group. Furthermore, none of these values is much more than one quarter of the lowest value between an included taxon and a taxon in one of the other large groups (389, plumariids to sierolomorphids), again indicating a large gap between the three groups already identified.

The second group (sphecids and apids) has somewhat greater internal variation (246), but the value is only about half the mean value for the entire study. Furthermore, this figure is also only about half of the lowest value between a member of this group and one of the others (489, sphecids to sierolomorphids), reemphasizing the presence of a large gap.

The third group contains 20 taxa and is more complex to analyze. The variation within this group is quite considerable, and the mean value of  $DT$  within the group (339) is insignificantly less than the minimal value between a member of this group and one of the other two (389, sierolomorphids to plumariids). The most distinct taxon included here is the formicids, which is more distinct from every other taxon (minimal  $DT$  is 373, to typhoctids, and mean is 507) than the

mean value for the group. It is also about as distinct within the group as the group is from one of the other groups. This suggests that the formicids may form a fourth group of the same rank as the

three already recognized. The scoliids and vespids are almost as distinct from other members of this group as are the formicids (minimal value is 323, vespids to typhocids) but less so from each other (183).

TABLE I. Occurrences ( $\Sigma i$ ) and numbers (k) of derived states, number of species subtended (S) and various distinctness measures (DF, DE, DC) for the internodes and final branches of the cladogram of Aculeata (Fig. 2).

Internode	$\Sigma i$	k	S <sup>a</sup>	DF	DE	DC
1-2	6.0	6	10030	129.42	0.41	53.06
2-Plumar.	17.0	22	20	46.07	0.42	19.35
2-3	4.0	4	10010	86.20	0.78	67.24
3-Bethyl.	1.0	1	10000	21.54	0.40	8.62
3-Scolcb.	12.0	12	10	25.80	0.78	20.12
1-4	6.0	6	58500	232.92	0.69	160.71
4-5	15.0	15	32000	476.25	0.63	300.04
5-Sphced.	3.0	3	12000	68.67	0.48	32.96
5-Apids	16.0	16	20000	434.24	0.49	212.78
4-6	5.0	5	26500	149.05	0.80	119.24
6-7	7.5	8	7700	148.12	0.46	68.14
7-8	10.5	11	5200	181.86	0.56	101.84
8-Sapygd.	4.0	4	150	21.24	0.66	14.02
8-9	12.5	13	5050	214.50	0.54	115.83
9-Myrmos.	6.0	7	50	22.08	0.55	12.14
9-Mutild.	9.0	9	5000	153.90	0.52	80.03
7-10	2.0	2	2500	27.14	0.38	10.31
10-Anthob.	1.5	2	100	6.96	0.31	2.16
10-11	1.0	1	2400	13.39	1.00	13.39
11-Thynnnd.	3.0	3	1000	30.00	0.21	6.30
11-12	3.5	4	1400	39.16	0.63	24.67
12-13	3.0	3	600	25.29	0.67	16.94
13-Myzind.	1.0	1	500	7.94	0.33	2.62
13-Methoc.	17.0	18	100	78.88	0.48	37.86
12-14	13.5	14	800	125.28	0.25	31.32
14-Tiphid.	3.0	3	700	26.64	0.68	18.12
14-Brachy.	11.0	14	100	51.04	0.36	18.37
6-15	3.0	3	18800	79.77	0.33	26.32
15-Sierol.	12.0	12	20	32.52	0.33	10.73
15-16	3.0	3	18780	79.68	0.67	53.38
16-17	7.0	7	3050	101.50	0.39	39.58
17-Pompil.	8.0	8	3000	115.36	0.39	44.99
17-Rhopal.	14.0	14	50	51.52	0.37	19.06
16-18	4.0	4	15730	100.32	0.31	31.10
18-19	7.0	7	15500	174.51	0.40	69.80
19-Formic.	18.0	18	12000	412.02	0.57	234.85
19-20	9.0	9	3500	136.62	0.77	105.20
20-Vespid.	10.0	10	3000	144.20	0.55	79.31
20-Scolid.	23.0	23	500	182.62	0.57	104.09
18-21	19.0	19	230	116.47	0.50	58.24
21-22	6.0	6	20	16.26	0.52	8.46
22-Typhoc.	3.0	3	10	6.45	0.26	1.68
22-Eotild.	4.0	4	10	8.60	0.38	3.27
21-23	14.5	17	210	86.13	0.54	46.51
23-Chypho.	8.5	9	100	39.44	0.42	16.56
23-24	16.0	18	110	76.64	0.75	57.48
24-Aptero.	5.5	6	100	25.52	0.61	15.57
24-Bradyn.	21.5	22	10	46.22	0.77	35.59

<sup>a</sup> Estimated number of species (including those yet to be described). Calculations utilize  $\sqrt[3]{S}$ .

TABLE II. Taxonomic distinctness (DT) for the taxa of Aculeata.

	SCOLEC.	BETHYL.	PLUMAR.	SPHECD.	APIDS	ANTHOR.	THYND.	MYZIND.	METHOC.	TRPHD.	BRACHY.	SAPYGD.	MYRMOS.	MUTILD.	SEROL.	POMPL.	RHOPL.	FORMIC.	YESPID.	SCOLD.	TYPHOC.	EOTILD.	CHYPHO.	APTERO.	BRADYN.
29																									
107	95																								
634	623	566																							
814	802	746	246																						
501	489	433	533	713																					
518	507	450	550	730	22																				
556	545	488	588	768	60	50																			
592	580	524	624	803	95	86	40																		
586	575	518	618	798	90	80	69	104																	
586	575	518	618	798	90	81	69	104	36																
604	593	536	636	816	128	146	184	219	214	214															
718	707	650	750	930	242	260	298	333	328	328	142														
786	775	718	818	998	310	328	366	401	396	396	210	92													
457	446	389	489	669	118	135	173	208	203	203	221	335	403												
585	573	517	616	796	245	262	300	336	330	330	348	462	530	149											
559	547	491	590	770	219	236	274	310	304	304	322	436	504	123	64										
836	824	768	868	1048	496	514	552	587	581	582	599	713	781	400	420	394									
785	774	717	817	997	446	463	501	536	531	531	549	663	731	350	370	344	419								
811	799	742	842	1022	470	488	526	561	556	556	574	688	756	374	395	369	444	183							
600	588	532	631	811	260	277	315	350	345	345	363	476	545	164	184	158	373	323	347						
601	590	533	633	813	261	279	317	352	347	347	365	478	547	165	186	160	375	324	349	5					
652	641	584	684	864	313	330	368	403	398	398	416	529	598	217	237	211	426	376	400	73	75				
709	697	641	741	921	369	387	425	460	454	455	473	586	654	273	293	268	482	432	457	130	131	90			
729	717	661	761	941	389	407	445	480	474	475	493	606	674	293	313	288	502	452	477	150	151	110	51		

These two may thus also form a separate group.

The remaining taxa form a paraphyletic group and show a wide range of variation, although no one taxon is minimally as distinct from any other as are the formicids, vespids and scoliids. Thus, the basal taxa on each of the three major branches involved have the following values: anthoboscids to sapygids—128; anthoboscids to sierolomorphids—118; sapygids to sierolomorphids—221. This indicates that these branches are not highly distinct, these values all being less than the mean value for all included taxa (280). When members at the extremes of the included branches are considered, however, it is seen that some of the taxa are highly distinct from each other (e.g., mutillids to bradybaenids, 674). Furthermore, each pair of taxa along these branches does not show great differentiation of its members, so that at no point is it possible to identify a further distinct group. Since a paraphyletic taxon should logically only be recognized if it is approximately as homogeneous as other recognized holophyletic taxa at the same categorical level, the extreme variability of this group suggests that it should not be recognized as such. Further subdivision is, however, impossible because of the absence of internal gaps. If the formicids, vespids and scoliids are again added in, it is found that the total variation within the group is only increased by about one-sixth (maximum is now 781, mutillids to formicids). This produces a holophyletic group only slightly more variable than the paraphyletic one, so that the recognition of this large holophyletic group is probably the best course of action. The Aculeata is thus considered to comprise three subgroups of equal categorical rank, which may be designated as superfamilies, viz., Bethyloidea, Sphecoidea and Vespoidea. This is somewhat reminiscent of the

suggestion by Bradley (1958) who proposed two superfamilies, Vespoidea (including those taxa here placed in the Bethyloidea) and Sphecoidea.

Within the Bethyloidea, in the absence of any detailed studies of the included taxa other than those of previous workers, it seems best to maintain the commonly accepted family groups (cf., Maa & Yoshimoto, 1961), Bethyloidea, Scolytoidea, Cleptidae, Chrysididae, Loboscelidiidae, Dryinidae, Embolemidae, Sclerogibbidae and Plumariidae. (Krombein, 1957 & *in litt.*, has suggested that the Cleptidae and Loboscelidiidae may more appropriately be considered to fall within the Chrysididae.) Various of these taxa contain few species with apparently relict distributions, probably indicative of a remote origin. For example, recent Scolytoidea occur in Brazil and Madagascar (Evans, 1963), and Plumariidae (including Heterogyninae) occur in arid areas in South America, South Africa and the Mediterranean area (Rhodes) (Bradley, 1972; Nagy, 1969a).

Within the Sphecoidea the two main taxa have been treated differently in the past. The wasp component has recently been considered to comprise a single family, the Sphecidae (Leclercq, 1954; Evans, 1964b) while the bees comprise nine families (Michener, 1965; Rozen, 1965; Roberts, 1973). Since both groups contain comparable numbers of species and appear to include an approximately equivalent range of phenetic variation, it seems reasonable to subdivide both groups to a similar degree. If this is done, the Sphecoidea may be considered to contain either two families (one of wasps and one of bees) or two groups each consisting of a number of families. Since an important function of a classification involves information retrieval, the size of the group involved is of some concern, for efficiency is lost if a group is very large. Based on this consideration, it is suggested that the



eight subfamilies of sphecids recognized by Evans (1964b) be considered valid taxa at the family level, and that the presently accepted bee families be retained at that level. The Sphecoidea then consists of the Ampulicidae, Sphecidae, Larridae, Mellinidae, Pemphredonidae, Astatidae, Philanthidae, Nyssonidae, Colletidae, Halictidae, Oxaeidae, Andrenidae, Melittidae, Fideliidae, Megachilidae, Anthophoridae and Apidae. The first eight may be included in an informal grouping, the Spheciformes, and the last nine in the Apiformes. (It is of some interest that, despite his suggestion in 1944 that the bees should be placed "as a division of the Sphecoidea," Michener has retained the superfamily "Apoidea" in his subsequent papers, illustrating that some collective term for "bees" is necessary.)

Despite the general absence of marked gaps within the Vespoidea, recognition of subtaxa, mainly on the basis of areas of low distinctness, is possible. Thus the six taxa above internode 7-10 show generally low mutual distinctness and a slightly higher minimal value to surrounding taxa. They may thus logically be recognized as a single taxon at the family level with the component taxa designated as subfamilies. The Tiphidae thus comprises the Anthoboscinae, Thynninae, Myzininae, Methochinae, Tiphinae and Brachycistidinae. Although many of the values are somewhat higher for the five taxa subtended by internode 18-21, the gaps between any of these and any member of the larger group are considerably greater. Here again it is probably appropriate to recognize these taxa as a group at the family level. The lowest value in the matrix is that between two members of this group, a figure so small (5) that the question arises as to whether recognition of these taxa as separate is justified. In the absence of convincing evidence to the contrary, recognition of these members at a very

low level is probably appropriate. The Bradynobaenidae thus comprises the Typhoctinae (with tribes Eotillini and Typhoctini), Chyphotinae, Apterogyninae and Bradynobaeninae.

The only other relatively low values (less than 100) are those between the pompilids and rhopalosomatids (64) and the myrmosids and mutillids (92). In both instances consideration should be given to inclusion of both taxa in the same family. In the case of the rhopalosomatids and pompilids this does not seem appropriate since the habits of the two groups are completely different (rhopalosomatids develop as ectoparasites of active crickets and pompilids store paralyzed spiders as larval provisions). The myrmosids and mutillids, however, have extremely similar habits, both being parasitoids of the prepupae or pupae of other Hymenoptera (see Knerer, 1973, e.g.). This suggests that they may be considered to fall in a single family, the Mutillidae (see section on Mutillidae below for details).

Each remaining taxon is best considered as valid at the family level at the least. The vespid group may additionally be considered to comprise three families (Masaridae, Eumenidae, Vespidae) as recommended by Richards (1962). Since the formicid group is highly distinctive within the Vespoidea, it also seems appropriate to recognize the Formiciformes informally to contain the family Formicidae, the remainder of the Vespoidea being the Vespiformes. (Incidentally, it is of some interest that a form more similar to *Sierolomorpha* than to *Anthobosca* seems to be indicated as the ancestral type that gave rise to ants; Anthoboscinae have in the past been considered to be the closest to the ancestral form, Wilson, Carpenter & Brown; 1967.)

The superfamily Vespoidea is therefore considered to contain the following 12

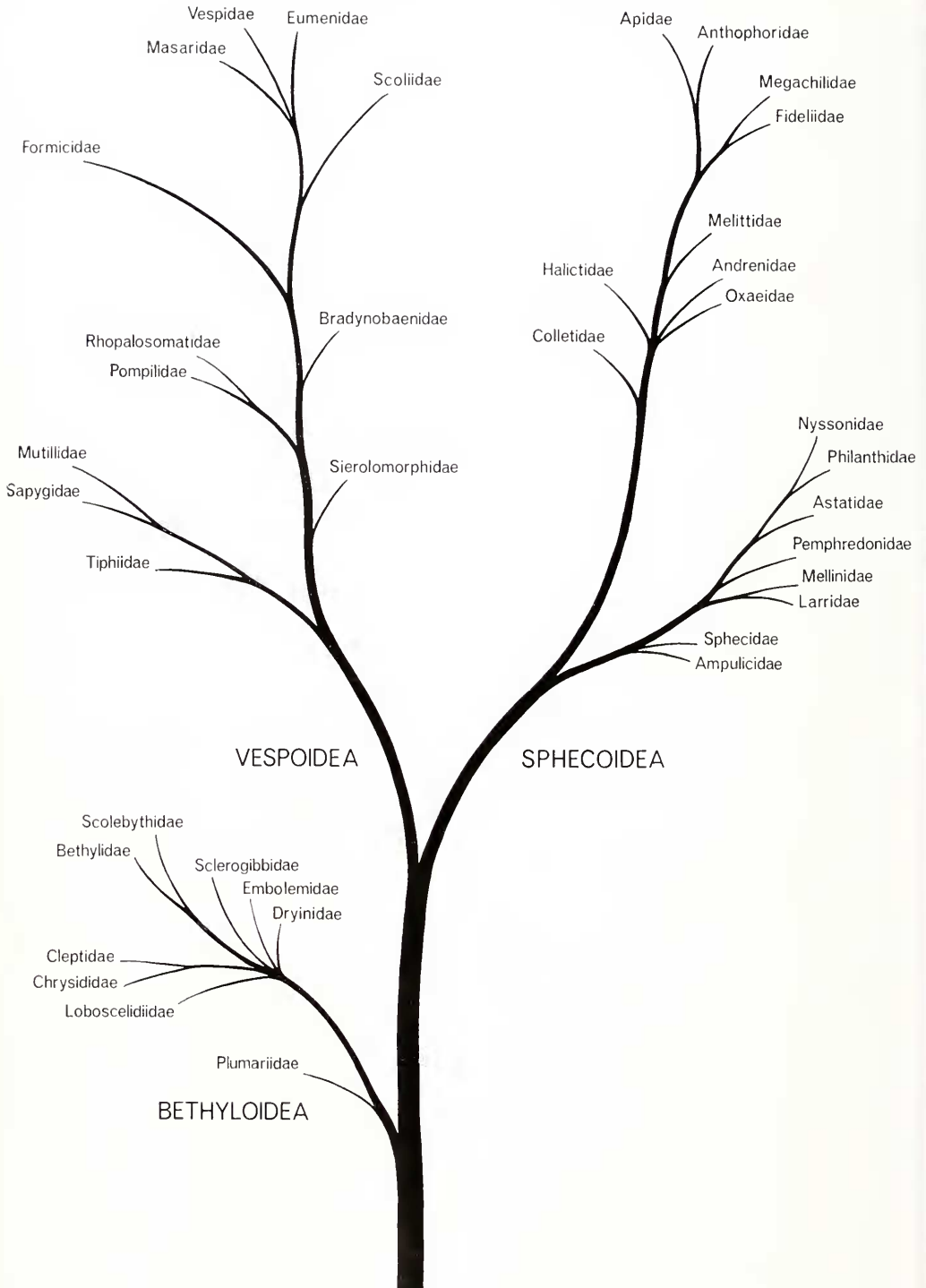


FIG. 67. Phylogeny of the families of Hymenoptera Aculeata (relationships within the Vespoidea from the present study; within the Sphecoidea from Michener, 1974, for the Apiformes, and Evans, 1964b, for the Spheciformes; within the Bethyloidea from the present study and personal impressions).

families: Tiphiiidae, Sapygidae, Mutillidae, Sicolomorphidae, Pompilidae, Ropalosomatidae, Scoliidae, Masaridae, Eumenidae, Vespidae and Bradynobaenidae in the Vespiformes, and Formicidae in the Formiciformes.

The phylogeny of the Aculeata to the level of family thus appears as in Fig. 67.

#### INVESTIGATION OF THE MYRMOSID-MUTILLID COMPLEX (MUTILLIDAE)

The methods used in the study of the myrmosid-mutillid group were similar to those utilized in the study of the entire Aculeata. Initially, all available specimens (approximately 10,000, in about 1250 species and including representatives of 89 per cent of the valid described genera and subgenera as well as many undescribed genera) were surveyed for about 50 characters, mainly ones which had been used previously to differentiate members at the generic and suprageneric levels. (The material examined is summarized in Table III. This is actually a highly conservative estimate since the extensive collections of many museums on four continents were also surveyed, but only the most significant specimens were borrowed and thus included in the figures given here.) This survey demonstrated that many characters were highly variable, and these were discarded. New characters were discovered and incorporated. On the basis of the initial survey, and considering published views such as those of Bischoff (1920-21) and Schuster (1947, 1949), members of 135 genera and subgenera of mutillids were tentatively grouped into 16 suprageneric complexes and these were surveyed with respect to 46 characters. At this point various genera (or subgenera) showed identical distributions of the character states and many such superfluous members were discarded, one genus generally being retained for each such set of con-

cordant states. Wagner trees (by electronic computer) and cladograms (by hand) were constructed, and characters having states with many independent origins or reversals were discarded. Additional characters were discovered and added, and further groups showing concordance of character states were reduced to representative genera. Representatives of three genera of myrmosids were added and a few additional characters were introduced as a result.

The machine- and hand-derived cladograms were then compared and refined as a few more characters were added, eliminated or coding was modified. Finally, identical cladograms based on 43 characters (involving 61 derived states) were derived both by the machine and by hand. When the characters were allocated to two data sets, one containing the 20 characters of females and the other those of males, and cladograms were derived using these data sets independently, the resulting schemes were fully compatible although not identical because of the lack of characters for females on two of the internodes. A final check was made that the character states differentiating each taxon on the tree were present in all the genera and subgenera represented by that taxon.

#### States of the Characters Considered

The 43 "best" characters used in the analysis of the myrmosid-mutillid complex are listed below, with comments on their evolutionary patterns. This is followed by a listing of the characters which were eliminated during the analysis, with the reasons for their elimination. In both cases characters of females are listed before those of males, the applicable sex being indicated by the prefixes F (female) and M (male). Even in cases where characters are apparently identical in the two sexes, they have been considered separately be-

TABLE III. Genera and subgenera of Mutillidae, including the approximate number of species examined. (\* indicates that the type species was seen. Information on synonymies and new sex associations will be presented elsewhere.)

MYRMOSINAE	Myrmosa (3 spp.*; ♂, ♀; incl. Ischioceras) Myrmosina (1 sp.*; ♂) Myrmosula (2 spp.*; ♂, ♀) Protomutilla (1 sp.; ♀)
<i>Not examined:</i> Krombeinella (incl. Paramyrmosa Suárez), Leiomyrmosa, Morysmula, Paramyrmosa Saussure.	
PSEUDOPHOTOPSIDINAE	Pseudophotopsis (10 spp.; ♂, ♀; incl. Alloneurion, Ephotomma, Sphinctomutilla André, 1899)
TICOPLINAE	Arcotilla (5 spp.*; ♂, ♀) Nanomutilla (3 spp.*; ♂, ♀) Smicromyrmilla (17 spp.; ♂, ♀)
<i>Not examined:</i> Ticopla.	
RHOPALOMUTILLINAE	Rhopalomutilla (13 spp.*; ♂, ♀)
SPHAEROPHTHALMINAE DASYLABRINI	Apteromutilla (4 spp.*; ♂, ♀; incl. Apterotilla) Brachymutilla (7 spp.*; ♂, ♀) Chrestomutilla (5 spp.*; ♂, ♀) Dasylabris (28 spp.*; ♂, ♀; incl. Allomutilla) Dasylabroides (21 spp.*; ♂, ♀) Seyrigilla (1 sp.*; ♀) Stenomutilla (16 spp.*; ♂, ♀; incl. Xenomutilla) Tricholabiodes (14 spp.*; ♂, ♀)
<i>Not examined:</i> Craspedopyga.	
SPHAEROPHTHALMINI PSEUDOMETHOCINA	Ancipitotilla (1 sp.*; ♂) Anomophotopsis (1 sp.*; ♂) Atillum (9 spp.*; ♂, ♀) Calomutilla (3 spp.*; ♀) Darditilla (10 spp.; ♂, ♀) Dimorphomutilla (6 spp.; ♂, ♀) Euspinolia (11 spp.*; ♂, ♀; incl. Reedia Ashmead) Gurisia (2 spp.*; ♀) Hoplocrates (15 spp.*; ♂, ♀; incl. Hoplomutilla André) Hoplognathoca (3 spp.*; ♀) Hoplomutilla Ashmead (18 spp.*; ♂, ♀; incl. Tilluma) Horcomutilla (6 spp.*; ♀) Invreicla (3 spp.*; ♀) Jamaitilla (1 sp.*; ♂, ♀) Lynchiatilla (4 spp.; ♂, ♀) Mammomutilla (1 sp.*; ♂) Mickelia (1 sp.; ♀) Myrmilloides (1 sp.*; ♂, ♀) Pappognatha (5 spp.; ♂, ♀) Patquiattilla (1 sp.*; ♀) Pertyella (6 spp.*; ♀) Pseudomethoca (23 spp.*; ♂, ♀; incl. Nomiaephagus) Scabratilla (1 sp.*; ♀) Sphinctopsis (33 spp.*; ♂, ♀; incl. Sphinctomutilla André, 1909) Tallium (13 spp.*; ♂, ♀) Vianatilla (1 sp.*; ♀)
<i>Not examined:</i> Allotilla.	

TABLE III. Genera and subgenera of Mutillidae, including the approximate number of species examined. (\* indicates that the type species was seen. Information on synonymies and new sex associations will be presented elsewhere.) (Continued.)

SPHAEROPHTHALMINA	<p>Acanthophotopsis (2 spp.*; ♂)</p> <p>Acrophotopsis (1 sp.*; ♂)</p> <p>Ascetotilla (8 spp.*; ♂, ♀)</p> <p>Bothriomutilla (1 sp.*; ♂, ♀)</p> <p>Cephalomutilla (7 spp.; ♀)</p> <p>Ceratophotopsis (2 spp.*; ♂)</p> <p>Cystomutilla (2 spp.*; ♂, ♀)</p> <p>Dasytilla (110 spp.*; ♂, ♀; <i>incl.</i> Bruesia, Pycnomutilla)</p> <p>Dilophotopsis (6 spp.*; ♂, ♀)</p> <p>Ephutomorpha <i>sensu stricto</i> (6 spp.*; ♀)</p> <p>Eurytilla (11 spp.*; ♂, ♀)</p> <p>Huacotilla (1 sp.; ♀)</p> <p>Leucopilomutilla (1 sp.*; ♂, ♀)</p> <p>Limaytilla (4 spp.*; ♂, ♀)</p> <p>Lomachaeta (6 spp.*; ♂, ♀)</p> <p>Lophomutilla (3 spp.*; ♀)</p> <p>Lophostigma (6 spp.; ♀)</p> <p>Micromutilla (7 spp.*; ♂, ♀)</p> <p>Morsyma (3 spp.*; ♂, ♀)</p> <p>Nanotopsis (1 sp.*; ♂)</p> <p>Neomutilla (3 spp.*; ♂, ♀)</p> <p>Odontophotopsis (16 spp.*; ♂; <i>incl.</i> Tetraphotopsis)</p> <p>Paramutilla (2 spp.?, *; ♂, ♀?)</p> <p>Periphotopsis (1 sp.*; ♂)</p> <p>Photomorphina <i>Schuster, 1952</i> (8 spp.; ♂, ♀; <i>incl.</i> Photomorphina <i>Schuster, 1958</i>)</p> <p>Photomorphus (3 spp.*; ♂, ♀)</p> <p>Photopsioides (5 spp.*; ♂, ♀)</p> <p>Physetapsis (1 sp.*; ♂)</p> <p>Photopsis (13 spp.*; ♂, ♀; <i>incl.</i> Agama <i>Blake</i>, Neophotopsis, Pyrrhomutilla)</p> <p>Protophotopsis (2 spp.*; ♂, ♀)</p> <p>Ptilomutilla (4 spp.*; ♀)</p> <p>Reedomutilla (4 spp.*; ♂, ♀; <i>incl.</i> Reedia <i>André</i>)</p> <p>Scaptodactyla (6 spp.*; ♂, ♀)</p> <p>Smicromutilla (1 sp.*; ♂, ♀)</p> <p>Sphaerophthalma (2 spp.*; ♂, ♀; <i>incl.</i> Sphaerophthalma)</p> <p>Suarezitilla (6 spp.; ♂, ♀)</p> <p>Tobantilla (4 spp.; ♂, ♀)</p> <p>Traumatomutilla (31 spp.*; ♂, ♀)</p> <p>Xenophotopsis (1 sp.*; ♂)</p> <p>Xystromutilla (6 spp.; ♂, ♀)</p>
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*Not examined:* Chasquitilla, Protophotopsiella, Xenomorphus.

*In addition to other scattered undescribed genera, representatives of at least 20 undescribed genera from the Australasian region, mainly Sphaerophthalmina but a few Pseudomethocina, were examined.*

## MYRMILLINAE

<p>Blakeius (2 spp.*; ♂, ♀; <i>incl.</i> Bisigilla)</p> <p>Ceratotilla (9 spp.*; ♂, ♀)</p> <p>Clinotilla (1 sp.*; ♂, ♀)</p> <p>Labidomilla (12 spp.*; ♂, ♀)</p> <p>Liomutilla (1 sp.*; ♀)</p> <p>Liotilla (1 sp.*; ♀)</p> <p>Myrmilla (10 spp.*; ♂, ♀; <i>incl.</i> Edrionotus, Eurygnathilla, Pseudomutilla, Rudia)</p> <p>Myrmotilla (1 sp.*; ♀)</p> <p>Odontotilla (9 spp.*; ♂, ♀)</p> <p>Platymyrmilla (1 sp.*; ♂, ♀)</p> <p>Pygomilla (6 spp.*; ♀)</p>
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TABLE III. Genera and subgenera of Mutillidae, including the approximate number of species examined. (\* indicates that the type species was seen. Information on synonymics and new sex associations will be presented elsewhere.) (Concluded.)

	Sigilla (1 <i>sp.</i> ; *; ♂, ♀)
	Spilomutilla (3 <i>spp.</i> ; ♂, ♀)
	Squamulotilla (26 <i>spp.</i> ; ♂, ♀)
	Viereckia (9 <i>spp.</i> ; *; ♂, ♀)
<i>Not examined:</i> Omotilla, Saganotilla.	
MUTILLINAE	
MUTILLINI	
MUTILLINA	Hadrotilla (1 <i>sp.</i> ; *; ♀)
	Mutilla (23 <i>spp.</i> ; *; ♂, ♀; <i>incl.</i> Barymutilla, Pycnotilla, Ronisia)
	Odontomutilla (40 <i>spp.</i> ; ♂, ♀; <i>incl.</i> Peringueya, Radoszkowskiius)
	Tropidotilla (4 <i>spp.</i> ; *; ♂, ♀)
<i>Not examined:</i> Physetopoda.	
SMICROMYRMINA	
	Antennotilla (4 <i>spp.</i> ; *; ♂)
	Artiotilla (1 <i>sp.</i> ; *; ♀)
	Aurcotilla (2 <i>spp.</i> ; *; ♂, ♀)
	Bisuleotilla (1 <i>sp.</i> ; *; ♂)
	Carinotilla (3 <i>spp.</i> ; ♂, ♀)
	Chrysotilla (4 <i>spp.</i> ; ♀)
	Corytilla (3 <i>spp.</i> ; ♂, ♀)
	Ctenotilla (15 <i>spp.</i> ; *; ♂, ♀; <i>incl.</i> Cephalotilla, Pseudocephalotilla)
	Dolichomutilla (7 <i>spp.</i> ; *; ♂, ♀)
	Eremomyrme (6 <i>spp.</i> ; ♂)
	Glossotilla (16 <i>spp.</i> ; *; ♂, ♀)
	Gynandrotilla (2 <i>spp.</i> ; ♂)
	Lophotilla (4 <i>spp.</i> ; ♂, ♀)
	Mimecomutilla (3 <i>spp.</i> ; *; ♂, ♀)
	Pristomutilla (10 <i>spp.</i> ; ♂, ♀)
	Promecilla (18 <i>spp.</i> ; *; ♂, ♀)
	Psammotherma (2 <i>spp.</i> ; *; ♂)
	Smicromyrme (100 <i>spp.</i> ; *; ♂, ♀)
	Spinulotilla (6 <i>spp.</i> ; *; ♂, ♀)
	Suleotilla (3 <i>spp.</i> ; *; ♂, ♀)
	Timulla (175 <i>spp.</i> ; *; ♂, ♀; <i>incl.</i> Lobotilla, Trogaspidia)
	Trispilotilla (5 <i>spp.</i> ; ♂, ♀)
<i>Not examined:</i> Hildebrandtia, Rhombotilla, Sylvotilla, Zeugomutilla. Chaetotilla probably also falls here.	
EPHUTINI	
	Ephuamelia (1 <i>sp.</i> ; ♂)
	Ephuchaya (1 <i>sp.</i> ; *; ♂)
	Ephuscabra (1 <i>sp.</i> ; *; ♂)
	Ephusuarezia (2 <i>spp.</i> ; ♂, ♀?)
	Ephuta (50 <i>spp.</i> ; *; ♂, ♀; <i>incl.</i> Ephutopsis)
	Xenochile (1 <i>sp.</i> ; ♂)
<i>Not examined:</i> Arcasina.	

cause the distribution of the various states often differs in the females from that in the males. (See below for treatment in calculations, however.) Some of the less useful characters that had been used in the study of the Aculeata and which differentiate the myrmosids and mutillids

(e.g., subtle differences in the form of the posterolateral angle of the pronotum, extent of the mesopleural sulcus, length of the metanotum, size of the seventh metasomal sternum and hypopygium, all in the male) were not included here at any stage. The system of coding for the vari-

ous states is as for the investigation of the Aculeata. The names of taxa are those used in the final classification resulting from consideration of these data. (The final cladogram appears after the figures of characters, as Fig. 92.)

CHARACTERS UTILIZED FOR DERIVATION  
OF THE FINAL CLADOGRAM

F1. *Ocelli*. Primitively, the ocelli are well-developed or at least readily distinguishable. F1.1—The ocelli are completely obliterated and indistinguishable.

Presence of ocelli is considered primitive because this is the condition found generally throughout the Aculeata including the taxa most closely related to the Mutillidae.

Loss of the ocelli in apterous forms is common throughout the Insecta. Such loss is characteristic of all Mutillidae except some Myrmosinae (ocelli present in species of *Myrmosa*) and a few species of *Pseudophotopsis* (Pseudophotopsidinae). Thus state F1.1 has been derived within the Myrmosinae and at least twice within the remaining Mutillidae, once within *Pseudophotopsis* and once on the line leading to all other Mutillidae. Nevertheless, the derived state appears only once on the tree, on internode 2-3. In view of its multiple derivations, state F1.1 cannot be considered strong evidence for the holophyletic nature of the Mutillidae above *Pseudophotopsis*, but indeed the presence of the primitive condition in many species of Myrmosinae and Pseudophotopsidinae serves to emphasize the basal position of those taxa.

F2. *Eye form*. Primitively, the compound eye is somewhat flattened in profile, merging smoothly with the surrounding cuticle, and is also broadly oval in outline. F2.1—The compound eye is highly convex in profile, strongly differentiated from the surrounding cuticle and approximately

hemispherical, being more or less circular in outline.

A flattened, ovate eye is considered primitive because this is the condition in most Aculeata and in particular those taxa most closely related to the Mutillidae (viz., Fedtschenkiinae, Anthoboscinae).

Although there is a tendency for the eye to be circular in a few groups where it is also reduced in size (e.g., *Rhopalomutilla*, *Nanomutilla*), the specialized hemispherical form of the eye has apparently evolved only once, in the Sphaerophthalmi, and is characteristic of almost all members of this tribe. In a few related genera (e.g., *Euspinolia*, *Tallium*, *Atillum*, *Hoplocrates*) the eye has become somewhat flattened once more although retaining some of the other characteristics of the tribe such as the basically circular shape. Despite this apparent partial reversal within the Sphaerophthalmi, state F2.1 provides strong evidence for the holophyletic origin of this taxon.

F3. *Eye pubescence*. Primitively, the compound eye is pubescent, bearing setae set into minute pores between the ommatidia. The setae may be prominent at relatively low magnification or they may be essentially indistinguishable although the pores may be discerned. F3.1—The compound eye is completely glabrous and all pores are lost.

A pubescent eye is considered primitive because most groups of Aculeata have eyes which are either obviously pubescent or which have well-developed pores bearing minute setae. In particular this is true of the Fedtschenkiinae and most Tiphidae, the taxa most closely related to the Mutillidae.

Loss of pubescence and pores in the compound eye has apparently occurred at least twice, in the Pseudophotopsidinae and on internode 3-4, so that the only groups with the eye prominently pubescent or with pores are the Myrmosinae

and Ticoplineae. Within the latter group *Areotilla*, *Nanomutilla* and *Ticopla* all have the eyes with dense and quite long setae (as do the Myrmosinae), whereas *Smicromyrmilla* has the setae reduced but still possesses a few pores in most species. The presence of the primitive state in the Ticoplineae is thus significant in emphasizing the relatively basal position of this taxon, rather than the derived state being useful in defining holophyletic groups.

F4. *Maxillary palpus*. Primitively, the maxillary palpus consists of six segments. F4.1—The maxillary palpus comprises only two segments.

A six-segmented maxillary palpus is considered primitive because this is the condition in most Aculeata, including the taxa most closely related to the myrmosid-mutillid group, and also in practically all members of this group.

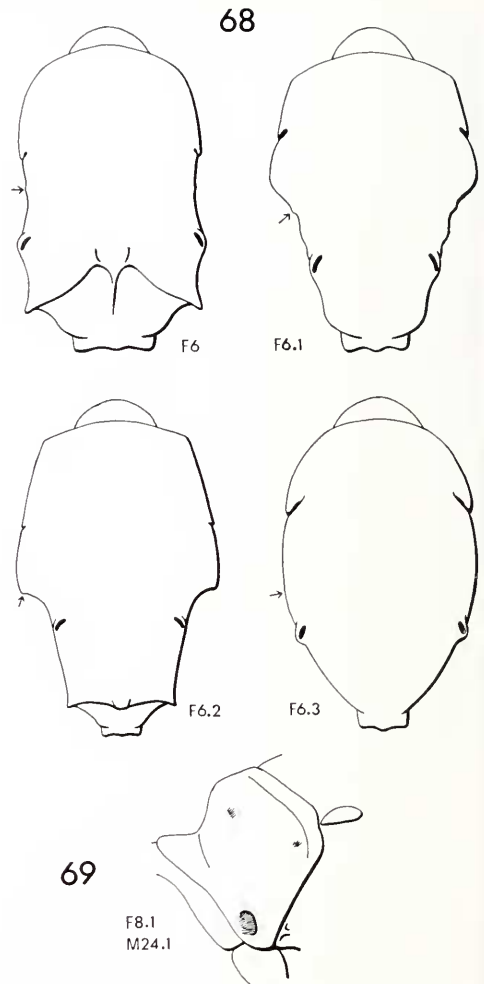
Reduction of the maxillary palpus in the female to two segments has occurred in only one genus, *Rhopalomutilla*, and so serves to emphasize the distinctness of the Rhopalomutillinae rather than to establish any higher groupings.

F5. *Labial palpus*. Primitively, the labial palpus consists of four segments. F5.1—The labial palpus is reduced to two segments.

A four-segmented labial palpus is considered primitive because this is the condition in almost all Aculeata, including those taxa most closely related to the Mutillidae, and also in most members of this family.

Reduction of the labial palpus to two segments in the female has occurred once only, in the Rhopalomutillinae, thus not providing any essential information on higher level groups.

F6. *Form of mesosoma* (Fig. 68). Primitively, the mesosoma has an approximately constant width although subtle variations may involve depression of the



FIGS. 68-69. Characters of Mutillidae. 68, mesosoma of female, dorsal view, showing primitive and derived states of form, with position of second spiracle arrowed (F6 based on *Areotilla*; F6.1 on *Sphaerophthalma*; F6.2 on *Rhopalomutilla*; F6.3 on *Ephuta*); 69, prothorax, lateral view, showing derived state of pronotal pit (F8.1, M24.1 based on *Pseudophotopsis*).

mesopleuron and/or lateral expansion of the propodeum. Thus the mesosoma is more or less parallel-sided, narrower at the mesopleural level than elsewhere or broader posteriorly than anteriorly. F6.1—The mesopleuron is protuberant at about half its length, predominantly as a result of broad development of the mesopleural ridge which is dorsally separated



from the prothoracic spiracle. The mesosoma thus broadens behind the prothoracic spiracle and then narrows from a point some distance anterior to the second mesosomal spiracle, the metapleural-propodeal region being narrower than the pronotum. F6.2—The metapleuron and lateral face of the propodeum are somewhat depressed and the mesopleuron is very slightly protuberant. The mesosoma thus broadens gently and evenly from the anterolateral angle of the pronotum to a point at the approximate level of the second mesosomal spiracle, behind which it is abruptly constricted. F6.3—The mesosoma is oval with the mesopleuron very slightly protuberant although the mesopleural ridge is undeveloped. The mesosoma is thus evenly broadened from the anterolateral region of the pronotum to the mesosomal midpoint and then evenly narrowed to the posterior region of the propodeum which is about as wide as the pronotum.

An approximately parallel-sided mesosoma is considered primitive because this is the condition in the Myrmosinae which are considered to occupy a basal branch on the cladogram on the basis of other characters. It is also the condition in some of the less-derived members of the Ticopliinae such as *Arcotilla* and *Nanomutilla*, this being a group with many other characters in the primitive states. The primitive state also includes some variations in mesosomal form that occur in various genera but do not characterize particular groups. The particular derived states considered seem to involve the most distinct modifications, each having originated independently.

Some of the variations included in the primitive type have occurred sporadically. For example, the mesopleuron is somewhat depressed in *Pseudophotopsis* (Pseudophotopsidinae), *Squamuloilla* (Myrmillinae) and *Aureoilla* (Mutillini), among

others; the propodeum is broadened in *Smicromyrmilla* (Ticopliinae), *Labidomilla* (Myrmillinae) and some *Timulla* (Mutillini). State F6.1, by contrast, is characteristic of a single group, the Sphaerophthalminae, having arisen on internode 5-6. It is thus a useful state establishing this group as holophyletic. Unfortunately, the strength of this state is slightly lessened by the fact that the mesopleuron is somewhat similarly expanded in *Odontomutilla* (Mutillini) in which, however, the propodeum is not markedly narrower than the pronotum. State F6.1 is also slightly modified in the Pseudomethocina, a subgroup of the Sphaerophthalmini, mainly by a slight dorsal flattening and anterior displacement of the mesopleural ridge.

State F6.2 is present only in *Rhopalomutilla* and state F6.3 is characteristic of the various members of the Ephutini only. These states are thus of minimal use in establishing higher groups. Actually the various forms of the mesosoma in the female are difficult to describe and are more distinct than might be indicated by the particular designation of derived states. Thus the Pseudophotopsidinae, Myrmillinae and Mutillini also have somewhat characteristic forms of the mesosoma although these are impossible to describe and code adequately.

F7. *Pro-mesonotal suture*. Primitively, the suture between the pronotum and mesonotum is freely articulating and is approximately straight. F7.1—The pro-mesonotal suture, although distinct, is fused and immovable and is also strongly curved so that the posterior margin of the pronotum is concave. F7.1.1—The pro-mesonotal suture is obliterated and indistinguishable (at least dorsally) or is barely indicated by a slight variation in sculpturing, when it is seen to be strongly curved.

An articulating pro-mesonotal suture is considered primitive because this is the condition in other Aculeata and almost

all male mutillids. An approximately straight posterior margin to the pronotum is also considered primitive because this is the situation in those taxa most closely related to the Mutillidae (viz., Fedtschenkiinae, Anthoboscinae).

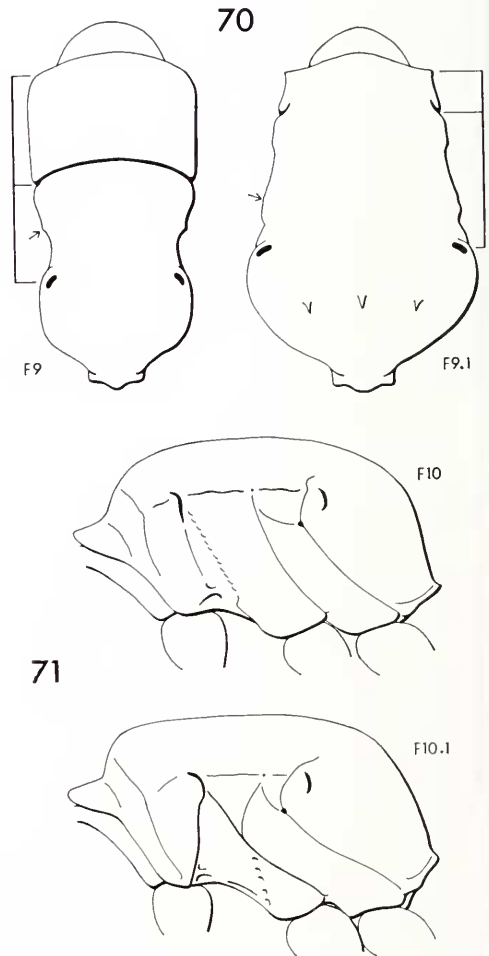
Fusion of the pro-mesonotal suture has occurred in the Aculeata only in the Mutillidae and is characteristic of the entire family except for the Myrmosinae. Strong concavity of the posterior margin of the pronotum is found in a number of the generally more derived taxa in the Aculeata and this condition is also characteristic of almost all the Mutillidae. Thus, state F7.1 arose once only, on internode 1-2, and is a very strong indicator of the holophyletic nature of the six higher subfamilies of the Mutillidae. Further obliteration of the pro-mesonotal suture (F7.1.1) has occurred on internode 2-3, thus providing further strong evidence of the holophyletic origin of the remainder of the family and emphasizing the low position of the Pseudophotopsidinae within the family. Although the position of the suture is sometimes discernible because of slight variations in sculpturing (e.g., some species of *Dasylabris*, *Neomutilla*), this condition is obviously more advanced than that in all species of *Pseudophotopsis* and cannot be confused with it, despite the fact that a few pseudophotopsidines have the fusion more developed than others.

F8. *Pronotal pit* (Fig. 69). Primitively, the pronotum is more or less evenly sculptured without any specialized pitlike structures. F8.1—The pronotum has a shallow pit at the ventral angle, which is filled with setae forming a structure similar to that on the first metasomal tergum in *Paratiphia* or the second metasomal tergum in some species of *Odontomutilla*, so that it may be analogous to the felt lines of the second metasomal segment.

A simple pronotum is considered prim-

itive because this is the condition in practically all Aculeata, including the taxa most closely related to the mutillids, and also in most of the Mutillidae.

The development of specialized ventral pits on the pronotum has occurred in only one genus, *Pseudophotopsis*, so that this is a strong character separating the Pseudophotopsidinae from the remaining Mutillidae but it is not of any use in



FIGS. 70-71. Characters of Mutillidae. 70, mesosoma of female, dorsal view, showing primitive and derived states of length of pronotum, with position of second spiracle arrowed (F9 based on *Myrmosa*; F9.1 on *Labidomilla*); 71, mesosoma of female, lateral view, showing primitive and derived states of meso-metapleural suture (F10 based on *Myrmilla*; F10.1 on *Smicromyrme*).

establishing holophyletic groups at the higher levels.

F9. *Length of pronotum* (Fig. 70). Primatively, the dorsolateral margin of the pronotum is about as long as the distance between the prothoracic and propodeal spiracles. F9.1—The dorsolateral margin of the pronotum is much shorter than (about two-thirds the length of) the distance between the prothoracic and propodeal spiracles.

A long pronotum (laterally) is considered primitive because the pronotum in *Fedtschenkia* and most of the generalized Aculeata such as the Anthoboscinae is quite long and well-developed. Shortening of the pronotum has occurred in various of the more derived groups of the Aculeata.

Shortening of the pronotum in the female has apparently occurred only once in the Mutillidae, on internode 4-5, and is thus characteristic of most members of the family, excepting only the four most basal subfamilies. This is thus quite a good indication of the holophyletic origin of the three higher subfamilies. Its strength is, however, perhaps diminished by the fact that a superficially similar derived state has occurred within the Myrmosinae (e.g., in *Myrmosula*), although here the apparent reduction in size of the pronotum appears to have resulted from a posterior displacement of the propodeal spiracle. The similarity to state F9.1 may thus be more apparent than real in this case.

This measure for describing the lateral shortening of the pronotum was chosen for convenience, but it cannot express the complex changes in proportion which occur in the mesosoma as a whole (such as have apparently occurred in *Myrmosula*). The change which has taken place on internode 4-5 is actually more distinct than might be thought from the description alone, and consideration of the mesosoma

as a whole strengthens the use of this character.

F10. *Meso-metapleural suture* (Fig. 71). Primatively, the meso-metapleural suture passes from a point just posterior to the mid-coxa dorsally directly to the second mesosomal spiracle, and is approximately straight. This suture is thus also separated from the dorsoventral mesopleural ridge. In some cases the meso-metapleural suture is slightly anteriorly curved and approaches the mesopleural ridge, usually if this ridge is dorsally separated from the prothoracic spiracle and thus somewhat posteriorly shifted. F10.1—The meso-metapleural suture passes anterodorsally from the mid-coxa and becomes continuous with the mesopleural ridge which is dorsally contiguous with the pronotal spiracle. The dorsal section of the meso-metapleural suture (between the mesopleural ridge and the second mesosomal spiracle) is at an acute angle to the ventral section. In many instances the dorsal section of the meso-metapleural suture and the ventral portion of the mesopleural ridge are obliterated so that there is an apparently continuous suture extending from a point just posterior to the mid-coxa anterodorsally to the prothoracic spiracle. [These modifications were first noted by Reid (1941) who considered the mesopleural ridge to be the prepectal suture. His interpretation of the evolutionary sequence was also slightly different since he considered the mesopleural ridge to be primitively separated from the prothoracic spiracle.]

An approximately straight meso-metapleural suture is considered primitive because this is the condition in most other members of the Aculeata, including those taxa most closely related to the Mutillidae, and also in mutillid males, especially those of the more generalized subfamilies (but see character M26).

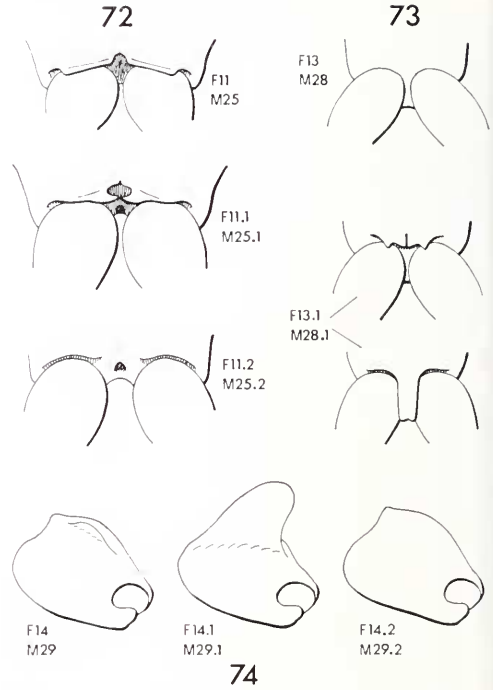
Strong angulation of the meso-metapleural suture is characteristic of all genera

of Mutillini except for *Odontomutilla* in which this state is approached but where the mesopleural ridge is separated from the prothoracic spiracle dorsally, this apparently secondary condition obscuring the situation. State F10.1 is thus shown on the cladogram on the branch leading to the Mutillini despite the fact that it is not definitely present in *Odontomutilla* (which falls into the Mutillini by virtue of a combination of different characters). This state is also considered to be good evidence for the holophyletic derivation of the Mutillini, the significance of which is increased by the fact that this is one of the largest tribes of the family.

F11. *Mesosternal teeth* (Fig. 72). Primitively, the mesosternum bears a simple transverse carina anterior to each mid-coxa. F11.1—The mesosternum has a pair of toothlike projections, one anterior to each mid-coxa, being elaborations of the primitive carinae. F11.2—The mesosternum is simple, without any protuberances or carinae.

A mesosternum with simple carinae is considered primitive because this is the condition in the Fedtschenkiinae and is the precursor to the state in the Tiphiidae, these being the taxa most closely related to the Mutillidae.

The presence of small dentate projections on the mesosternum anterior to the coxae in females (F11.1) is characteristic only of *Pseudophotopsis*. Since this is an autapomorphic state, it does not provide any data on higher groupings. By contrast, loss of the carinae (F11.2) is characteristic of the females of Myrmosinae and also of the remaining Mutillidae, the latter derivation having occurred on internode 2-3. Since this state has occurred twice, it is not a strong indicator on which to base higher groups. Furthermore, a state somewhat similar to the primitive one has been redeveloped in some of the more highly derived members of the



FIGS. 72-74. Characters of Mutillidae. 72, posterior region of mesosternum, ventral view, showing primitive and derived states of mesosternal teeth (F11, M25 based on *Myrmosa*, ♂; F11.1, M25.1 on *Pseudophotopsis*, ♂; F11.2, M25.2 on *Areotilla*, ♂); 73, posterior region of metasternum, ventral view, showing primitive and derived states of metasternal process (F13, M28 based on *Myrmosa*, ♂; F13.1, M28.1 on *Dasytubris*, ♂, and *Hoplocrates*, ♂, top to bottom; 74, hind coxa, showing primitive and derived states (F14, M29 based on *Pseudophotopsis*, ♂; F14.1, M29.1 on *Myrmosa*, ♂; F14.2, M29.2 composite).

Sphaerophthalmina (e.g., *Ascetotilla* and some other genera in the "*Ephutomorpha* complex"), further weakening this state.

F12. *Contiguity of mid-coxae*. Primitively, the mid-coxae are contiguous mesally. F12.1—The mid-coxae are slightly separated and do not contact each other along the midventral line.

Contiguous mid-coxae are considered primitive because this is the condition in the Myrmosinae and Pseudophotopsidinae, which are the taxa considered to be the most basal on the cladogram on the basis of other characters.

Separated mid-coxae are characteristic of the entire Mutillidae except for Myrmosinae and Pseudophotopsidinae, so that state F12.1 provides good evidence for the holophyletic nature of the Mutillidae above internode 2-3. The strength of this character is, however, somewhat diminished by the fact that the middle coxae show various degrees of contiguity or separation throughout the Aculeata.

F13. *Metasternal process* (Fig. 73). Primatively, the metasternum is simple and flattened anteromesal to the hind coxa. F13.1—The metasternum bears a process anteromesal to each hind coxa. This may be a transverse carina, or the mesal extremity of this carina may be produced as a tooth which may be fused with the process of the opposite side to form a single mesal projection on the metasternum.

A simple metasternum is considered primitive because this is the condition in the Sapygidae, the sister group of the Mutillidae. Although there is slight development of a mesal longitudinal ridge in *Fedtschenkia*, this is developed anterior to the position of the protuberances involved in state F13.1 and is furthermore obviously not a paired structure. A simple metasternum is also present in the Myrmosinae, which forms a basal branch of the cladogram on the basis of other characters.

A dentate metasternum is characteristic of the entire family Mutillidae except for the Myrmosinae. Since this state is apparently unique in the Aculeata, it provides very good evidence of the holophyletic nature of the group above internode 1-2. This may, however, not be quite as strong as at first considered since the metasternum is apparently somewhat plastic elsewhere in the Aculeata and has been modified in various ways.

F14. *Hind coxal tubercle* (Fig. 74). Primatively, each hind coxa bears a carinate tubercle dorsally. F14.1—Each hind coxa

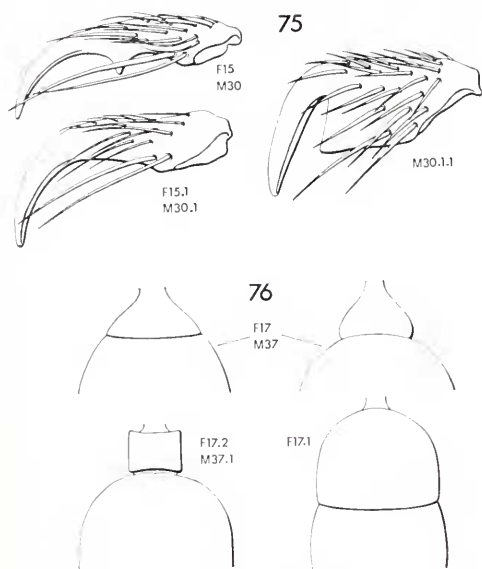
bears a lamellate process dorsally. F14.2—Each hind coxa is simple, without any dorsal tubercle or lamella.

The presence of a carinate tubercle on the hind coxa is regarded as primitive because this is the condition in the Fedtschenkiinae, which is the group most closely related to the Mutillidae, and also in most of the basal members of the Mutillidae (so considered in the light of other characters).

Elaboration of the hind coxal carina into a lamellate process (F14.1) is uniquely characteristic of the Myrmosinae and is thus an important character state differentiating this group. Loss of the coxal tubercle is often difficult to establish with certainty since the tubercle is never very highly developed even when obviously present. Nevertheless, a hind coxal tubercle is definitely present in *Pseudophotopsis*, *Areotilla* and *Smicromyrmilla*. The small size of *Nanomutilla* makes determination very difficult, but a tubercle does appear to be present in this genus and in *Rhopalomutilla* also. Thus state F14.2 appears to have evolved once only, on internode 4-5. In view of the difficulties involved in determining the condition of the hind coxa and since it seems likely that such insignificant structures may have been lost on various occasions, the presence of state F14.2 should probably not be regarded as of great significance in establishing the holophyly of the Mutillidae above internode 4-5. Instead, the presence of the primitive state in three subfamilies serves to emphasize the basal position of these.

F15. *Tarsal claws* (Fig. 75). Primatively, each tarsal claw bears a sharp tooth about halfway along the ventral margin. F15.1—Each tarsal claw is simple, the ventral tooth having been lost.

A toothed tarsal claw is considered primitive because this is the condition in most Aculeata and in particular those taxa most closely related to the Mutillidae, a



FIGS. 75-76. Characters of Mutillidae. 75, claw, showing primitive and derived states (F15, M30 based on *Pseudophotopsis*, ♀; F15.1, M30.1 on *Mutilla*, ♀; M30.1.1 on *Rhopalomutilla*, ♂); 76, base of metasoma, dorsal view, showing primitive and derived states of form of first segment (F17, M37 composite; F17.2, M37.1 based on *Ephuta*, ♀; F17.1 on *Rhopalomutilla*, ♀).

single tooth being present in Fedtschenkiinae and many Tiphidae.

Simple tarsal claws in the female are characteristic of the entire subfamily Myrmosinae and all other Mutillidae except for the Pseudophotopsidinae, having been derived in the latter instance on internode 2-3. State F15.1 has thus arisen on two occasions within the myrmosid-mutillid group, and also elsewhere in the Aculeata; its presence is thus not particularly good evidence for the association of most of the Mutillidae into a single holophyletic group. Instead, the presence of the primitive condition in *Pseudophotopsis* again serves to emphasize the basal position of this taxon.

F16. *Arolium*. Primitivesly, the arolium is well-developed, forming a definite padlike structure between the tarsal claws and being distinct under magnifications of 50× or less. F16.1—The arolium is obliterated

(or at least extremely reduced) so that no such structure is distinguishable, even at magnifications of 100×.

A well-developed arolium is considered primitive because this is the condition in most Aculeata, including the Fedtschenkiinae and Anthoboscinae, those groups most closely related to the Mutillidae.

Complete loss of arolia has occurred on a single occasion, this condition being characteristic of the Myrmosinae. Within the other Mutillidae there is some variation in the degree of development of the arolia. These are most reduced (but nevertheless still distinct) in, for example, *Pseudophotopsis* (Pseudophotopsidinae) and *Reedomutilla* (Sphaerophthalmina).

F17. *Form of first metasomal segment* (Fig. 76). Primitivesly, the first metasomal segment (especially the tergum) is gradually and evenly broadened posteriorly and merges more or less smoothly in contour with the second. Although it may be somewhat constricted apically and narrower than the second, the first segment is never predominantly cylindrical (parallel-sided). F17.1—The first metasomal segment (notably the tergum) is much enlarged and almost parallel-sided, approximately as broad as the second segment and more than half its length. F17.2—The first metasomal segment, and especially the tergum, forms a constricted cylinder which is much narrower than and less than one quarter the length of the second segment.

A flaring first metasomal segment is considered primitive because this is the most widespread form amongst the Aculeata and in particular those taxa most closely related to the Mutillidae.

Both derived states are uniquely characteristic of single taxa on the cladogram. F17.1 is present only in the Rhopalomutillinae and F17.2 characterizes the tribe Ephutini. Since these are autapomorphic states, they do not provide useful informa-

tion on the grouping of the higher taxa but merely emphasize the specializations of the particular taxa involved.

F18. *Base of first metasomal tergum* (Fig. 77). Primitively, the first metasomal tergum is simple basally without any lateral protuberances. F18.1—The first metasomal tergum bears a pair of protuberances, one on each side, at the base, forming "auricles" which tend to cup the apex of the propodeum.

A simple first metasomal tergum is considered primitive because this is the condition in most Aculeata, and in par-

ticular in those taxa which are most closely related to the Mutillidae (viz., Fedtschenkiinae, Anthoboscinae).

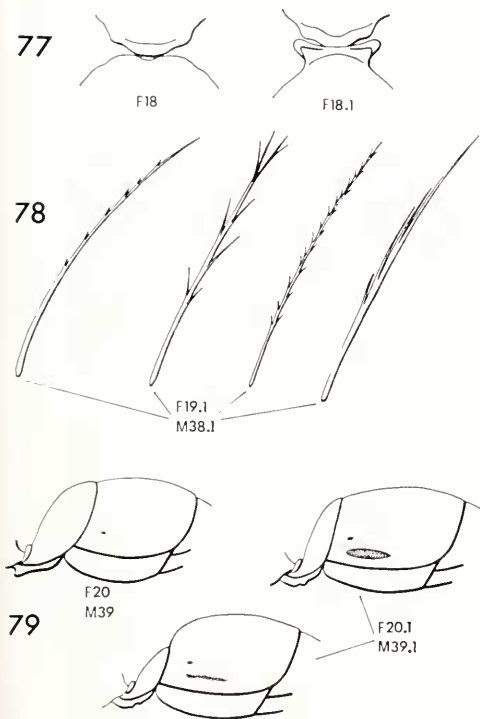
The development of auricles has apparently occurred only once. These structures are present in all members of the Mutillidae except for the Myrmosinae, so that state F18.1 was apparently derived on internode 1-2. The degree of development of the auricles varies, but they are smallest in the groups below internode 4-5, except for *Pseudophotopsis* where they are quite large. (This may in part be a result of the generally large body size of these species; the ancestral form may have been relatively small, if "Cope's Rule" is applicable—Stanley, 1973.)

F19. *Pubescence of first metasomal tergum* (Fig. 78). Primitively, all the pubescence is composed of simple, smooth setae. F19.1—Some erect setae at the base of the first metasomal tergum are plumose or subplumose, bearing fine branches. Much of the pubescence elsewhere on the body may also be plumose.

Simple pubescence is considered primitive because this is the condition in most Aculeata, including those groups most closely related to the Mutillidae.

Development of plumose pubescence has apparently occurred on a single occasion, being characteristic of the entire tribe Sphaerophthalmini. A few scattered genera within this group appear to have lost the plumosity, however (e.g., *Euspinolia*, *Atilium*, *Hoplocrates*, *Neomutilla*, *Cephalomutilla*, *Traumatomutilla*). Despite these few apparent reversals, the presence of state F19.1 is considered strong evidence for the holophyletic origin of the tribe Sphaerophthalmini. Although some species of *Stenomutilla* (Dasylabrini) have setae with trifurcate apices, their condition is unlike that in the Sphaerophthalmini and thus does not diminish the significance of this state.

F20. *Tergal felt line* (Fig. 79). Primi-



FIGS. 77-79. Characters of Mutillidae. 77, articulation of meso- and metasoma of female, dorsal view, showing primitive and derived states of base of first metasomal tergum (F18 based on *Myrmosa*; F18.1 on *Pseudophotopsis*); 78, seta from first metasomal tergum, showing derived state of pubescence (F19.1, M38.1 based on *Cystomutilla*, *Dasymutilla*, *Reedomutilla*, *Bothriomutilla*, left to right); 79, anterior region of metasoma, lateral view, showing primitive and derived states of tergal felt line (F20, M39 based on *Areotilla*, ♀; F20.1, M39.1 on *Odontomutilla*, ♀, and *Smicromyrme*, ♀, top to bottom).

tively, the second metasomal tergum is simple, without any development of specialized lateral felt lines or other secretory structures. F20.1—The second metasomal tergum bears a specialized felt line with recumbent setae and secretory pores, laterally on each side.

The absence of felt lines is considered primitive because this is the condition in most Aculeata, and in particular in the Sapygidae and Tiphiidae, those groups most closely related to the Mutillidae. Felt lines of similar form occur elsewhere only in the Bradynobaenidae, although some primitive bees (various Colletidae) possess foveae on the second metasomal tergum in a similar position, and these may be analogous to felt lines. The detailed anatomy of the felt lines in Mutillidae and Chyphotinae (Bradynobaenidae) has recently been elucidated by Debolt (1973).

A tendency toward development of felt lines on the second metasomal tergum appears to be characteristic of the family Mutillidae except for the Myrmosinae, although the actual development of such lines has apparently occurred on two occasions, once in *Pseudophotopsis* and again on internode 4-5. The presence of the felt line in a relatively basal taxon (Pseudophotopsidinae) as well as most higher members, indicates that its development is probably a general tendency in the family (at least above Myrmosinae). Since a tergal felt line has secondarily been lost in some higher genera (e.g., *Stenomutilla*, many *Ephuta*), it may be that the absence of the line is secondary in Ticoplinae and Rhopalomutillinae also. In both these groups there are, however, no traces of even rudimentary development of a felt line. It is thus more parsimonious to consider state F20.1 to have been fully expressed on two occasions rather than for it to have been developed on internode 1-2 and then to have been lost on two subsequent occasions (in the Ticoplinae and

Rhopalomutillinae). Nevertheless, the "tendency toward" development of a tergal felt line may be visualized as having been uniquely derived on internode 1-2 (as in the above investigation of Aculeata), this being a fairly strong state uniting most Mutillidae. (The development of felt lines seems to be correlated with the derived states of characters F53r, F54r, M79r and M80r, which apparently do not occur in the Myrmosinae, so that the tendency toward development of felt lines is considered to have been established after the divergence of the Myrmosinae.)

M21. *Eye form*. Primitively, the compound eye in the male is somewhat flattened in profile, merging smoothly with the surrounding cuticle. M21.1—The compound eye is highly convex in profile, strongly differentiated from the surrounding cuticle and approximately hemispherical.

A flattened eye is considered primitive because this is the condition in most Aculeata and in particular those taxa most closely related to the Mutillidae (viz., Fedtschenkiinae, Anthoboscinae).

The specialized hemispherical form of the eye in the male parallels the development of a similar eye form in the female (F2.1) quite closely. Thus, all members of the Sphaerophthalmini have hemispherical eyes in the male also, except that *Cystomutilla* has this state somewhat less well-developed than in most of the other genera. In addition, the group including *Euspinolia*, *Tallium*, *Atillum* and *Hoplocrates* also has the eyes less protuberant than other Sphaerophthalmini, as in the females. In contrast to the females, the males of *Tricholabiodes* (Dasylabrini) also have well-developed and protuberant eyes, although they are less nearly circular than in the Sphaerophthalmini. This means that if state M21.1 evolved once only, then the Sphaerophthalmini and *Tricholabiodes* share a common ancestor not also

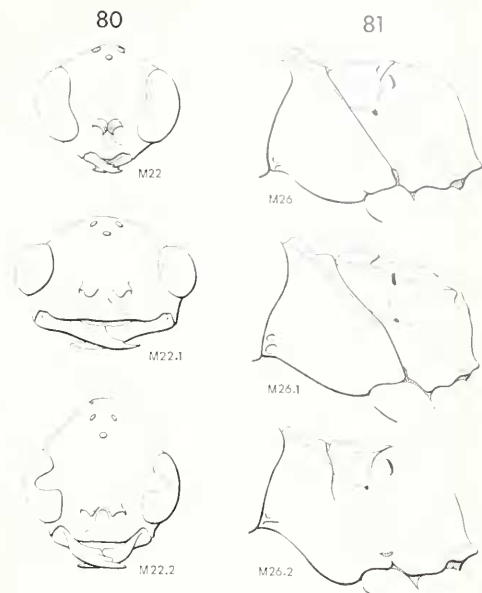


shared with the remaining Dasylabrini. Alternatively, state M21.1 may have arisen twice, once in the ancestral Sphaerophthalmini and again in *Tricholabiodes*. Although there are no good characters indicating holophyly of the Dasylabrini, it seems that forms similar to *Tricholabiodes* (all the species of which are nocturnal and highly specialized) would probably have been too specialized to have given rise to the Sphaerophthalmini. Two separate derivations of state M21.1 thus seem the more probable. Independent development of this condition in *Tricholabiodes* was probably associated with their nocturnal habit since other nocturnal Aculeata often have the eyes larger and more protuberant than do their relatives (e.g., Brachycistidinae in the Tiphidae, *Megalopta* in the halictid bees, and even *Pseudophotopsis* and *Eremomyrme* elsewhere in the Mutillidae to a lesser extent). Despite the uncertainty regarding the exact pattern of evolution of this character, state M21.1 provides quite good evidence for the holophyletic origin of the Sphaerophthalmini.

M22. *Eye shape* (Fig. 80). Primitively, the compound eye is broadly oval with the inner margin sinuately concave. M22.1—The compound eye is subcircular with the inner margin approximately evenly convex. M22.2—The compound eye is broadly oval with the inner margin strongly incised and emarginate, the angle of the emargination at its apex being less than  $90^\circ$ .

A broadly oval eye with sinuate inner margin is considered primitive because this is the condition in most Aculeata and in particular in those groups (such as Fedtschenkiinae and most Tiphidae) which are most closely related to the Mutillidae.

An approximately circular compound eye with a convex inner margin in the male is characteristic only of the Sphaerophthalmini, so that state M22.1 apparently



FIGS. 80-81. Characters of Mutillidae. 80, head of male, anterior view, showing primitive and derived states of eye shape (M22 based on *Smicromyrmita*; M22.1 on *Ascetotilla*; M22.2 on *Rhopalomutilla*); 81, meso- and metapleura and propodeum of male, lateral view, showing primitive and derived states of meso-metapleural suture (M26 based on *Pseudophotopsis*; M26.1 on *Aretotilla*; M26.2 on *Squamulotilla*).

arose only once on the cladogram. However, a few genera (such as *Euspinolia* and *Tallium*) have eyes which are almost circular but with the inner margins very slightly sinuate. A few members of the Dasylabrini (such as *Apteromutilla*, *Brachymutilla* and *Dasylabroides*) also have the inner margins of the eyes convex although the eyes are not as nearly circular as in the Sphaerophthalmini. Actually, there seems to be a tendency toward reduction in the size of the eyes in many of the higher Mutillidae and especially in the Sphaerophthalminae, which sometimes makes accurate determination of the occurrence of state M22.1 difficult. Nevertheless, this does seem to be a fairly good indicator of the holophyletic nature of the Sphaerophthalmini.

Emargination of the eye (M22.2) is characteristic of the entire subfamily Mutillinae and thus arose on internode 7-8. A similar condition is, however, present in Rhopalomutillinae. *Areotilla* shows a marked tendency toward development of this state also, with *Smicromyrmilla* and *Nanomutilla* (all three Ticoplineae) having the inner margin slightly more deeply sinuate than in *Pseudophotopsis*. Thus the presence of state M22.2 in the Mutillinae is not as useful an indication of the association of the members of this subfamily as could be wished, although it is obvious that its occurrences in the Rhopalomutillinae and *Areotilla* were independent of its origin in the Mutillinae.

M23. *Eye pubescence*. This character shows the same pattern of evolution and occurrence as in the female (F3), with the derived state (M23.1) having occurred in all members of the Mutillidae except the Myrmosinae and Ticoplineae. It thus provides no additional information on higher groupings.

M24. *Pronotal pit* (Fig. 69). This character shows the same pattern of occurrence as in the female (F8), with the derived state (M24.1) being characteristic of the Pseudophotopsidinae. This condition was one of the main characters used by Schuster (1950) to associate the sexes of this group.

M25. *Mesosternal teeth* (Fig. 72). The states of this character are as for the female (F11), although their distribution is slightly different. The elaboration of the mesosternal carinae into dentate projections in the male (M25.1) coincides with a similar development in the female (F11.1), being found only in *Pseudophotopsis*. By contrast, the obliteration of the carinae (M25.2) has occurred in all other Mutillidae except for most Myrmosinae, unlike the situation in females. Thus, simple carinae are developed in the males

of *Myrmosa* but they have been lost in *Myrmosula* (the condition in *Protomutilla* is unknown). State M25.2 thus appears only once on the cladogram, on internode 2-3. Nevertheless, its parallel occurrence within the Myrmosinae tends to weaken it, so that it should not be considered a particularly good indicator of the holophyletic nature of the Mutillidae above internode 2-3. It appears that there is never any redevelopment of mesosternal carinae or teeth in the males of the more highly derived Mutillidae similar to that in the females of *Ascetotilla* and other genera related to *Ephutomorpha*. A few genera in the *Sphaerophthalma* complex (such as *Odontophotopsis*) bear mesosternal teeth of varying types, but these are placed anterior to the position of the primitive carinae and are obviously not an expression of this character.

M26. *Meso-metapleural suture* (Fig. 81). Primitively, the meso-metapleural suture is approximately straight. M26.1—The meso-metapleural suture is curved posteriorly so that the hind margin of the mesopleuron is convex. M26.2—The meso-metapleural suture is sinuate so that the hind margin of the mesopleuron is concave over at least the ventral half and is convex dorsally; the metapleuron thus appears to be expanded anteriorly below the endophragmal pit.

An approximately straight meso-metapleural suture is considered primitive because this is the condition in those Aculeata most closely related to the Mutillidae (viz., Fedtschenkiinae, Anthoboscinae) and also in those groups considered on the basis of other characters to be the most basal on the cladogram (i.e., Myrmosinae, Pseudophotopsidinae).

A posteriorly curved meso-metapleural suture (M26.1) is found only in *Areotilla*, *Nanomutilla* and *Smicromyrmilla* so that this forms a very good characteristic establishing the Ticoplineae as a holophyletic

group (the condition in *Ticopla* is, however, unknown to me). A sinuate meso-metapleural suture (M26.2) is characteristic of the entire Mutillidae except for the Myrmosinae, Pseudophotopsidinae and Ticoplinae. This state apparently arose uniquely on internode 3-4 and is thus a very useful indicator of the holophyletic origin of the four higher subfamilies.

M27. *Meso-metapleural "bridge"* (Fig. 82). Primitively, the meso- and metapleura are closely associated but not fused at any point. The anterior margin of the metapleuron is simple ventrally with only a slight protuberance approaching the hind margin of the mesopleuron but not contacting it. M27.1—The metapleuron ventrally bears a marked tubercle which

is fused with a similar protuberance on the mesopleuron, so that a "bridge" is formed between these pleura which are additionally fused for some distance over their ventral halves.

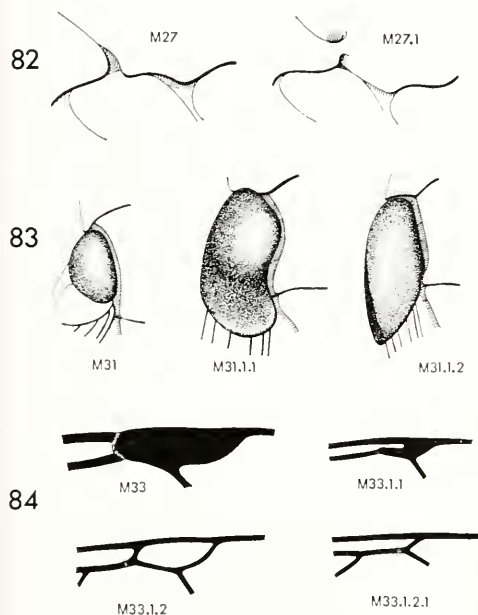
A simple metapleuron not fused to the mesopleuron is considered primitive because this is the condition in most Aculeata and in particular in the Fedtschenkiinae and Tiphiiidae, those taxa most closely related to the Mutillidae. The development of a slight protuberance at the anteroventral angle of the metapleuron has not occurred in these related taxa but is actually another derived state associating the myrmosid-mutillid complex, and is thus considered primitive for the complex.

The development of a meso-metapleural "bridge" is characteristic of all Mutillidae except for the Myrmosinae, Pseudophotopsidinae and Ticoplinae, in which there is merely a small tubercle ventrally on the metapleuron. Thus state M27.1 apparently arose on internode 3-4, strongly associating most of the Mutillidae into a holophyletic group.

M28. *Metasternal process* (Fig. 73). The evolution and occurrences of the various states of this character are the same as in the female (F13). Thus state M28.1 is characteristic of the entire Mutillidae except for the Myrmosinae, apparently having arisen on internode 1-2.

M29. *Hind coxal tubercle* (Fig. 74). The pattern of modifications of this character is the same as for the female (F14), so that state M29.1 is characteristic of the Myrmosinae, and M29.2 has apparently arisen on internode 4-5. As in the female, a tubercle is never very well-developed in the male, except in Myrmosinae, so that determination of the state involved is often difficult, reducing the significance of this character.

M30. *Tarsal claws* (Fig. 75). Primitively, each tarsal claw bears a sharp tooth about



FIGS. 82-84. Characters of Mutillidae. 82, ventral region of meso-metapleural suture of male, lateral view, anterior to left, showing primitive and derived states of meso-metapleural "bridge" (M27 based on *Myrmosa*; M27.1 on *Squamulotilla*); 83, left tegula of male, dorsal view, showing primitive and derived states (M31 based on *Myrmosa*; M31.1.1 on *Odontomutilla*; M31.1.2 on *Ephuta*); 84, pterostigma of forewing, showing primitive and derived states (M33 based on *Pseudophotopsis*; M33.1.1 on *Viereckia*; M33.1.2 on *Dolichomutilla*; M33.1.2.1 on *Ephuta*).

halfway along the ventral margin. M30.1—Each tarsal claw is simple, the ventral tooth having been lost. M30.1.1—Each tarsal claw is broadened into a dentate lamella basally but is simple apically, so that it appears cleft.

A tarsal claw with a single distal ventral tooth is considered primitive because most aculeates have toothed claws and this is the condition in the Fedtschenkiinae and many Tiphidae, the groups most closely related to the Mutillidae. The subsequent development of a basal lamella is considered to be derived from the simple condition because this state is unlike that in most other Aculeata and also because it appears in only one sex of a single genus within the Mutillidae, a genus which seems on the basis of other characters to have arisen on the cladogram above the point of derivation of state M30.1.

Loss of the tooth on the tarsal claws of the male does not quite coincide with this condition in the female (F15.1). Thus, the males of Myrmosinae have armed claws whereas the females do not. State M30.1 has thus apparently arisen only once, on internode 2-3, being characteristic of all Mutillidae except for Myrmosinae, Pseudophotopsidinae and Rhopalomutillinae. The last group is uniquely characterized by possession of state M30.1.1. Thus state M30.1 is useful as an indicator of the holophyletic nature of the Mutillidae above Pseudophotopsidinae while M30.1.1 merely serves to emphasize the distinctness of the Rhopalomutillinae and does not aid in establishing higher groupings. This interpretation of the origin of the condition in the male of *Rhopalomutilla* differs from that of Schuster (1947) who considered it to be primitive and comparable to that in *Pseudophotopsis*.

M31. Tegula (Fig. 83). Primitively, each tegula is an evenly convex, subcircular sclerite with its hind margin not attain-

ing the level of the transscutal suture. M31.1—Each tegula is posteriorly produced so that its hind margin exceeds the level of the transscutal suture, the tegula being subovate. M31.1.1—The hind margin of the elongate tegula is reflexed, forming a posterior upcurved rim. M31.1.2—The elongate tegula is longitudinally angulate basally so that it has two distinct surfaces approximately perpendicular to one another, at least anteriorly.

A short, evenly convex tegula is considered primitive because this is the condition in most Aculeata, including those groups most closely related to the Mutillidae (viz., Fedtschenkiinae, Anthoboscinae).

Elongation of the tegula (M31.1) is characteristic of the entire subfamily Mutillinae and has apparently arisen on the cladogram only once, on internode 7-8. Elongate tegulae are found in scattered genera elsewhere, however, but in these their form is generally not identical to that in the Mutillinae. Thus *Smicromyrmilla* has tegulae which reach the transscutal suture but do not exceed it, and *Nanomutilla* and *Areotilla* have tegulae which do exceed this line but which are mesally curved posteriorly, those in *Areotilla* in particular being very elongate and more or less reniform, a condition unlike that in the Mutillinae. (These modifications do, however, indicate that there is a tendency toward some type of tegular elongation in the Ticoptinae as a whole, but this does not appear on the cladogram. It does not fall into any of the designated states since it is rather indefinite.) A few of the more highly derived members of the Sphaerophthalmina, like *Bothriomutilla*, also have the tegulae posteriorly produced to or slightly beyond the level of the transscutal suture, but in these this appears to be partly the result of anterior displacement of this suture laterally, and the tegulae are not as elongate as in the

Mutillinae. The presence of state M31.1 is thus considered quite good evidence for the holophyletic origin of the Mutillinae.

State M31.1.1 is present only in the tribe Mutillini, although a few of the more derived members of the Sphaerophthalmina such as *Bothriomuilla* exhibit a similar tendency toward reflexion of the posterior margin of the tegula. Also, a few genera of Mutillini such as *Ctenotilla* and *Mimecomutilla* show a secondary reversal of this state with the hind margin of the tegula not upturned but forming a more or less extensive flat area. Despite these few anomalies, state M31.1.1 appears to be a strong indicator of the holophyletic nature of the tribe Mutillini.

State M31.1.2 is uniquely characteristic of the tribe Ephutini and is not approached elsewhere in the Mutillidae, thus providing good evidence of the holophyletic nature of this tribe but not proving useful in the establishment of any higher groupings.

M32. *Extent of venation of forewing.* Primitively, the venation of the forewing attains the distal margin of the wing membrane or ends only a very short distance from it. M32.1—The venation of the forewing is obliterated apically so that the longitudinal veins do not reach the distal margin of the membrane but end a considerable distance from it; although there may be dark lines which do almost attain the margin, these are merely pigimentary and not differentiated cuticular structures.

Venation attaining the apical margin of the forewing is considered primitive because this is the condition in those groups most closely related to the Mutillidae [viz., Sapygidae (although venation slightly retracted in *Fedtschenkia*) and Anthoboscinae].

Retraction of the venation of the forewing to end a considerable distance from the apical margin of the wing is charac-

teristic of the entire family Mutillidae except for the Myrmosinae, and thus apparently arose on internode 1-2. Although this is a unique derivation here, a similar condition has occurred in various other groups of Aculeata, including some Tiphidae, thus weakening this state somewhat as an indicator of the holophyletic nature of most of the Mutillidae. Instead its absence serves to emphasize the basal position of the Myrmosinae.

M33. *Pterostigma* (Fig. 84). Primitively, the pterostigma is entirely heavily sclerotized and thus not cell-like. M33.1—The pterostigma has the sclerotization reduced, somewhat more so anteriorly than posteriorly, so that it appears as a small cell bounded basally by vein SC and with vein R much heavier than vein C. M33.1.1—The pterostigma is apparently formed entirely by the relatively heavy vein R, the free section of vein SC being lost. M33.1.2—The pterostigma is entirely desclerotized, with all the bounding veins of approximately equal width. M33.1.2.1—The pterostigma is absent as a result of the loss of the free section of vein R (or its fusion with vein SC) eliminating any cell.

A completely sclerotized pterostigma is considered primitive because this is the condition in most Aculeata, including those taxa most closely related to the Mutillidae (e.g., Fedtschenkiinae, Anthoboscinae).

A pterostigma with the sclerotization reduced anteriorly (M33.1) is not found in any extant members. Since all the taxa subtended by internode 5-7 show some degree of pterostigmal desclerotization, all with conditions which are logically derivable from a state such as M33.1, this state may have arisen uniquely on this internode. State M33.1 is thus apparently a good indicator of the holophyletic nature of the group comprised of the Myrmillinae and Mutillinae, despite the fact that this

state is hypothetical. There is actually a tendency toward a similar development in *Protophotosis* (Sphaerophthalmina) although in this genus the reduction of sclerotization is more even, veins R and C being approximately equally heavy, both heavier than any of the other veins.

Loss of vein SC is characteristic of the entire subfamily Myrmillinae, although this state (M33.1.1) is not very obvious in some members where the reduction of sclerotization is not very marked (e.g., *Viereckia*) and the loss of vein SC merely results in a basal emargination of the pterostigma. Since this state is uniquely characteristic of all members of the subfamily, it is useful in establishing the holophyletic nature of the Myrmillinae but does not aid further in higher groupings.

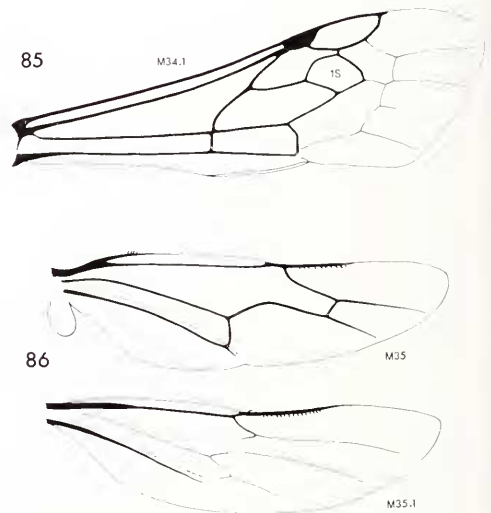
Complete desclerotization of the pterostigma (M33.1.2) is found only in the Mutillinae and is thus a strong indicator establishing the holophyly of the group, having arisen on internode 7-8. Some slight uncertainty is introduced by the fact that the Ephutini is characterized by complete loss of the pterostigma, although this condition seems logically more readily derivable from a state such as M33.1.2 rather than from the primitive condition. Loss of the pterostigma in the Ephutini (M33.1.2.1) has apparently occurred as a result of the elimination of its apical region, whether by loss of vein R or by its fusion with vein SC cannot be established. In any case it is apparent that vein SC is retained since the "crossvein" joins vein SC+R just distal to the weak point in vein SC+R. This point is at the base of the pterostigma, just proximal to vein SC, in other mutillids. This loss of the pterostigma provides a strong indication of the holophyletic nature of the Ephutini. A superficially similar loss of the pterostigma has occurred in *Odontomutilla* (Mutillina) but in this case it is apparently the result of the obliteration of the free section of

vein SC since the "crossvein" joins vein "SC+R" at a point some distance distal to the weak point in vein "SC+R."

M34. *Forewing cell 1S* (Fig. 85). Primitively, cell 1S (second submarginal) is sessile anteriorly, sharing a section of vein S with cell R (marginal). M34.1—Cell 1S is petiolate anteriorly, not reaching cell R (crossvein r-s reaches vein S distal to the junction of vein S and crossvein 1s-m).

A sessile cell 1S is regarded as primitive because this is the condition in most Aculeata, including those taxa most closely related to the Mutillidae (e.g., Fedtschenkiinae, Anthoboscinae).

A petiolate cell 1S is found only in the Ticoplinae where it is characteristic of all the genera (except perhaps for *Ticopla* where cell 1S is apparently lost). This state thus provides very good evidence of the holophyletic nature of this subfamily but does not aid further in higher level groupings. Elsewhere, state M34.1 is approached within the Myrmosinae (*Myrmosa* has cell 1S anteriorly acute and



FIGS. 85-86. Characters of Mutillidae. 85, forewing of male, showing derived state of cell 1S (M34.1 based on *Areotilla*); 86, hind wing of male, showing primitive and derived states of jugal lobe (M35 based on *Myrmosa*; M35.1 on *Areotilla*).

barely reaching cell R although not actually petiolate).

M35. *Jugal lobe* (Fig. 86). Primitively, the hind wing bears a small but well-differentiated jugal lobe basally. M35.1—The jugal lobe is completely lost so that the hind wing has a smooth posterior margin.

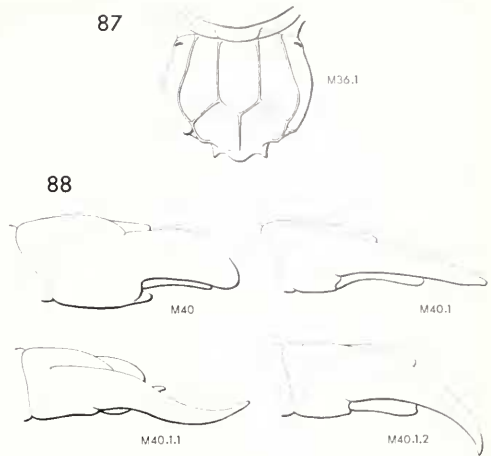
Presence of a jugal lobe is considered primitive because this is the condition in most Aculeata, including the Fedtschenkiinae and Anthoboscinae, i.e., those taxa most closely related to the Mutillidae.

The complete absence of a jugal lobe in the hind wing is characteristic of the entire Mutillidae except for the Myrmosinae and Pseudophotopsidinae. This state has thus apparently arisen on internode 2-3 and provides strong evidence for the holophyletic nature of the higher Mutillidae, despite the fact that a similar condition has occurred elsewhere in the Aculeata (e.g., in Bethyloidea).

M36. *Propodeal disc* (Fig. 87). Primitively, the propodeal disc is fairly heavily and evenly sculptured, often reticulately so. M36.1—The disc of the propodeum bears four subparallel longitudinal carinae linked posteriorly by a zig-zag transverse carina.

An evenly sculptured propodeal disc is considered primitive because this is the condition in those Aculeata most closely related to the Mutillidae (viz., Fedtschenkiinae, Anthoboscinae) and in most members of the Mutillidae.

A characteristic pattern of carinae on the disc of the propodeum is most highly developed in *Nanomutilla* (and *Ticopla*) and slightly less so in *Areotilla*. In *Smicromyrmilla* the fully winged species have similar carinae on the anterior region of the disc but the apterous species have the sculpturing modified so that the carinae are lost. Although a few species of *Rhopalomutilla* show a superficially similar condition (differing in detail, however), this pattern of sculpturing is considered



FIGS. 87-88. Characters of Mutillidae. 87, posterior region of mesosoma of male, dorsal view, showing derived state of propodeal disc (M36.1 based on *Nanomutilla*); 88, posterior region of male genitalia, lateral view, showing primitive and derived states of gonostylus (M40 based on *Pseudophotopsis*; M40.1 on *Nanomutilla*; M40.1.1 on *Protophotopsis*; M40.1.2 on *Antennotilla*).

to be present in these genera only, and thus is useful in associating them into the holophyletic subfamily Ticoplinae. (Nagy, 1970, however, cited this as a character in which *Ticopla* was similar to some Bethyloidea, although the pattern differs in detail in the groups involved.)

M37. *Form of first metasomal segment* (Fig. 76). Primitively, the first metasomal segment (especially the tergum) is evenly expanded from base to apex and is only slightly constricted apically so that it is not highly differentiated from the rest of the metasoma. Although it may be somewhat constricted apically and narrower than the second, the first segment is never predominantly cylindrical (parallel-sided). M37.1—The first metasomal segment (notably the tergum) is approximately cylindrical and short, being highly differentiated from the remainder of the metasoma.

An evenly dilated first metasomal segment is considered primitive because this is the condition in most Aculeata, including those taxa most closely related to the

Mutillidae (e.g., Fedtschenkiinae, Anthoboscinae), and also in most mutillids.

The development of a cylindrical, parallel-sided first metasomal segment in the male follows the same pattern as a similar development in the female (F17.2), being characteristic only of the Ephutini and providing a strong indication of the holophyly of that tribe but not providing additional information above that supplied by the female.

M38. *Pubescence on first metasomal tergum* (Fig. 78). The development of plumose pubescence in the males (M38.1) exactly parallels that in the females (F19.1), being characteristic of the entire Sphaerophthalmini except for a few genera in which plumosity has apparently been lost secondarily. This strengthens the importance of this state in establishing the Sphaerophthalmini as a holophyletic group, but does not provide more information on groupings than that given by females.

M39. *Tergal felt line* (Fig. 79). The pattern of development of a tergal felt line in the male is exactly the same as that in the female (F20), the derived state being present in the Pseudophotopsidinae and above internode 4-5 except for a few species. The tendency toward expression of state M39.1 may thus be considered to have been established on internode 1-2, although actual expression has occurred on at least two occasions. This state does not provide any additional information on higher groupings beyond that provided by females, but does serve to strengthen the conclusions based on that in the female.

M40. *Gonostylus* (Fig. 88). Primitively, each gonostylus is about twice as long as high, being lamellate with a rounded apex. M40.1—Each gonostylus is at least three times as long as its basal height, being approximately straight and tapered so that the apex is acute. M40.1.1—Each acute gonostylus is upcurved at the apex.

M40.1.2—Each acute gonostylus is downcurved apically.

A broad, rounded gonostylus is considered primitive because this is the condition in various of the more generalized groups of the Aculeata (e.g., Plumariidae, Sierolomorphidae) and especially in those taxa most closely related to the Mutillidae, such as Fedtschenkiinae and Anthoboscinae.

The development of an acute gonostylus (M40.1) has apparently occurred on a single occasion on the cladogram, on internode 2-3, since this condition is characteristic of all Mutillidae except for Myrmosinae and Pseudophotopsidinae. There are, however, a few instances in which somewhat of a reversal has occurred, so that in *Brachymutilla* (Dasylabrini), *Atillum* and *Hoplocrates* (both Pseudomethocina) the gonostyli are fairly broad and their apices are somewhat rounded, a similar but less marked tendency being shown in *Hoplomutilla*, *Myrmilloides* (both Pseudomethocina) and *Ctenotilla* (Smicromyrmina). Although state M40.1 is best placed on internode 2-3, *Nanomutilla* (Ticoplineae) has gonostyli which are narrowed but with apices which are somewhat blunt. In sum, the gonostyli in *Nanomutilla* appear to be more similar to those of the higher Mutillidae than to *Pseudophotopsis*, however. Thus the possession of narrow, acute gonostyli is quite a good characteristic associating the Mutillidae above internode 2-3 into a holophyletic group. In the Myrmosinae, however, a somewhat similar development has taken place in some members of the genus *Myrmosa*, although *Myrmosula* has gonostyli of the primitive type.

Dorsal curvature of the gonostylar apex (M40.1.1) is characteristic of the entire subfamily Sphaerophthalminae and is present in all members of that taxon except for a few specialized genera in which the gonostylus has been further modified and



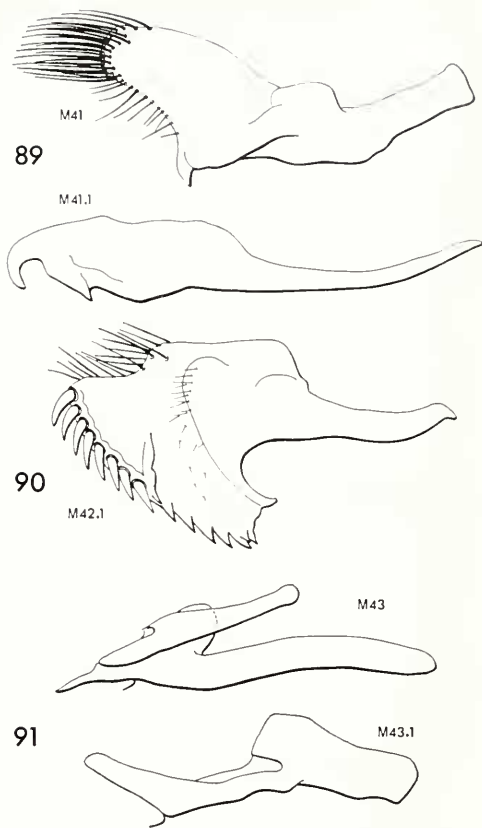
the apex is more or less straight (e.g., *Hoplomotilla*, *Myrmilloides*, *Atillum*, *Hoplocrates*, *Lomachaeta*). Although the apical curvature of the gonostylus may often be rather subtle, this seems to be a useful state for associating the Sphaerophthalmiinae in a holophyletic group, having arisen on internode 5-6.

Ventral curvature of the apex of the gonostylus (M40.1.2) is characteristic of the entire branch bearing both the Myrmillinae and Mutillinae although the degree of curvature is somewhat reduced in *Ctenotilla* (Smicromyrmina). This is thus a useful state establishing that these two subfamilies form a holophyletic group. Although *Nanomutilla* in the Ticopliinae has the gonostylus approximately straight, both *Areotilla* and *Smicromyrmilla* have the gonostyli strongly ventrally curved but with the conformation of the gonostyli in other respects unlike that of the myrmilline-mutilline group. This occurrence thus almost certainly represents an independent but somewhat similar modification of the gonostylus and does not materially weaken the significance of state M40.1.2 on internode 5-7.

**M41. Gonapophysis IX** (Fig. 89). Primatively, each gonapophysis IX has the apex much produced dorsally and posteriorly into a marked lobe and bears a tooth about halfway along the ventral margin. M41.1—Each gonapophysis IX has the dorsal apical lobe much reduced or lost and bears a tooth on the apical half of the ventral margin.

A gonapophysis IX with a large dorsal lobe apically is considered primitive because this is the condition in the Fedtschenkiinae, the group most closely related to the Mutillidae, and also in the Myrmosinae which forms a basal branch of the cladogram on the basis of other characters.

The form of the gonapophysis IX is somewhat more complex than can be con-



FIGS. 89-91. Characters of Mutillidae. 89, right gonapophysis IX of male, lateral view, anterior to right, showing primitive and derived states (M41 based on *Myrmosa nigriceps*; M41.1 on *Areotilla* sp.); 90, right gonapophysis IX of male, lateral view, anterior to right, showing derived state of gonapophyseal spines (M42.1 based on *Pseudophotopsis ?continua*); 91, right volsella, mesal view, anterior to left, showing primitive and derived states of digitus (M43 based on *Dasymutilla nigripes*; M43.1 on *Areotilla* sp.).

cisely described, but, basically, each has lost the dorsal lobe or has it greatly reduced in all taxa except the Myrmosinae, so that state M41.1 has apparently evolved once, on internode 1-2. Actually the form of the dorsal lobe in the Fedtschenkiinae is slightly different from that in the Myrmosinae where it often seems to be more strongly developed distally. Within the Myrmosinae its form differs also, being a large lamella often bearing long marginal setae in *Myrmosa*; it is non-setose in

*Myrmosula* but with a large apical ventral tooth, so that its condition appears to be more similar to that in both the Fedtschenkiinae and other Mutillidae.

M42. *Gonapophyseal spines* (Fig. 90). Primitively, each gonapophysis IX does not bear any articulating spines but is merely armed with one or more simple cuticular teeth ventrally. M42.1—Each gonapophysis IX bears stout spines articulating at the base along the distal ventral margin in addition to simple cuticular teeth.

Simply toothed gonapophyses IX are considered primitive because this is the condition in the group most closely related to the Mutillidae (i.e., Fedtschenkiinae) and also in almost all mutillids.

A gonapophysis IX with stout, articulating spines is found only in *Pseudophotopsis*. This is thus a good state establishing the Pseudophotopsidinae as a highly differentiated taxon, but it does not provide any information on higher groupings. Although such stout spines are unique to *Pseudophotopsis*, they may actually be modified setae such as are present in similar positions on the gonapophysis IX in most Mutillidae.

M43. *Digitus* (Fig. 91). Primitively, the volsella of the male genitalia comprises both a cuspis and a digitus. M43.1—The volsella consists of only the cuspis, the digitus having been obliterated.

A volsella with both digitus and cuspis is considered primitive because this is the condition in most Hymenoptera, including those taxa most closely related to the Mutillidae.

A digitus is present in practically all Mutillidae although it is often somewhat reduced and apparently not movable relative to the cuspis. In both the Ticoplineae and Rhopalomutillinae, however, the digitus has been completely lost, apparently independently in these two subfamilies,

the volsella otherwise appearing quite different in these taxa. Nevertheless, the presence of state M43.1 is quite a useful characteristic associating at least three genera in the Ticoplineae (the condition in *Ticopla* is unknown to me).

#### CHARACTERS REJECTED FOR DERIVATION OF THE FINAL CLADOGRAM

The following characters were considered but were rejected for the construction of the final cladogram, for various reasons. Some showed a high incidence of parallel or convergent derivations which lessened their usefulness. Others could not be described unequivocally in terms of one or a few states which could be readily distinguished. Instead they varied gradually, making it impossible to include them in the formal scheme. Other characters were considered and used early in the study before it had been established that the Mutillidae as then constituted was actually a polyphyletic group. When the Typhoctinae, Apterogyninae and Chyphotinae (Bradynobaenidae) had been removed from the Mutillidae, these characters became invariant, even after the Myrmosinae had been added to the study. Further characters were found to vary only within the final tribal or other divisions which were used as the basic taxa in the cladogram, and thus did not provide any information on higher groupings at the tribal level or above.

Of course most of these characters do provide useful information which was utilized mainly early in the investigation to obtain indications of probable groupings. Many will also be found useful in establishing groups within the final taxa used in the cladogram. However, the limitations of each have to be borne in mind at each stage.

Each character is briefly described below and the reasons for its rejection are given. The numbering is continuous with

that for the characters utilized, but the suffix "r" indicates rejection.

F44r. Absence (primitive) or presence (derived) of laterally flattened, lanceolate setae in the female.

This character varies only within the tribe Sphaerophthalmini in which those genera in the Pseudomethocina possess the derived state, as do other genera scattered in the Sphaerophthalmina. This character is thus variable within the group, provides no information on higher groupings at the levels involved in the cladogram and is also somewhat equivocal in that the degree of modification of the setae varies, making the determination of setae as lanceolate or not difficult in many cases.

F45r. Compound eye large (primitive) or small (derived).

Although relatively large eyes are retained in most members of the Mutillinae as well as the Pseudophotopsidinae and Myrmosinae, most members of the Sphaerophthalminae have the eyes reduced in size, as do many Myrmillinae, the Rhopalomutillinae and some Ticoplinae. There have been many parallel and convergent derivations of small eyes, and it is impossible to define the two states unequivocally.

F46r. Compound eye with ommatidia individually convex and differentiated (primitive) or with entire surface smooth and ommatidia undifferentiated (derived).

The derived state is found only within the Sphaerophthalmini (where it is developed in many of the genera of the Sphaerophthalmina and a few of those in the Pseudomethocina) and in *Tricholabiodes* in the Dasylabrini. Although the two states can be defined reasonably unequivocally, the derived state has occurred (or has been reversed) on many parallel occasions, thus not delimiting any groupings.

F47r. Antennal socket simple (primitive)

or with dorsomesal antennal tubercle (derived).

After removal of the Typhoctinae, Apterogyninae and Chyphotinae from the Mutillidae, all members of the myrmosid-mutillid complex possess the derived state.

F48r. Scape approximately straight and relatively short (less than 1.5 times as long as thick) (primitive) or sigmoid and more than twice as long as thick (derived).

All members of the myrmosid-mutillid complex have the derived state, the primitive scape being found in some of the genera that were excluded from the Mutillidae.

F49r. First flagellar segment subequal in length to the second (primitive) or more than twice the length of the second (derived).

Apart from a few members of the Myrmillinae, the derived state is found only in various members of the Sphaerophthalmini, where it is most commonly developed in the Pseudomethocina. This character shows numerous parallel and convergent derivations and also is incapable of unequivocal formulation.

F50r. Antenna with 12 (primitive) or 13 (derived) segments.

Only two genera possess the derived state (*Atillum* and *Hoplocrates* in the Pseudomethocina) so that this is of no use in establishing groups at the tribal (or even the subtribal) level.

F51r. Absence (primitive) or presence (derived) of a ventral excision forming a basal tooth on the mandible.

Although most members show the primitive state, the derived state appears in scattered genera throughout the Mutillidae so that many parallelisms and convergences are involved.

F52r. Mesosomal pleura approximately flat or convex (primitive) or markedly concave (derived).

Although the derived state is particularly characteristic of the Myrmillinae, it also occurs in one or more members of the Myrmosinae, Ticoplinae and Mutillinae and thus shows some parallel and convergent developments. The states are also difficult to define and identify unequivocally.

F53r. Lateral face of pronotum dorsally without (primitive) or with (derived) a small tubercle bearing fine setae and perhaps secretory pores.

Although the derived state appears to be characteristic of the entire Mutillidae except for the Myrmosinae, an unequivocal decision on the state involved, especially in small species, is often impossible because of the small size and minimal differentiation of this structure. The tubercle may be analogous to the felt line of the second metasomal segment.

F54r. Anterior face of pronotum dorsally without (primitive) or with (derived) a short transverse ridge bearing fine setae and perhaps secretory pores.

As for the previous character, the derived state is apparently characteristic of the entire Mutillidae except for the Myrmosinae, but certainty is impossible. This structure may also be analogous to the felt line of the second metasomal segment.

F55r. Pronotum with posteroventral margin distinct so that pronotum is well-differentiated from mesopleuron (primitive) or with posteroventral margin obliterated so that pronotum and mesopleuron are not differentiated (derived).

The primitive state is generally present in the Pseudophotopsidinae, Mutillini and many Sphaerophthalmini; the derived state is found in the other groups, generally differing in details in the different taxa. This means that many of the higher taxa can be characterized by detailed formulations of the type of derived state involved in each. Nevertheless, it is difficult to do

this unequivocally. These states also would provide no information on supratribal groupings. Furthermore, there is much variation in the degree of expression of these derived states, especially in the Sphaerophthalmini.

F56r. Mesopleuron dorsally protuberant (primitive) or depressed (derived).

Although the derived state is generally characteristic of the Mutillini (except for *Odontomutilla*) and Pseudophotopsidinae, it is also present in a few other genera so that it has occurred in parallel or convergently on various occasions. Furthermore, the range of variation present precludes accurate delimitation of these states.

F57r. Mesopleural ridge with ventral (often carinate) section anterior to (primitive) or dorsal to midpoint of (derived) mid-coxae.

Although the derived state tends to be characteristic of the Ticoplinae, unequivocal determination of the state is often difficult because of intermediates and also because of lack of development of the ridge.

F58r. Ventral section of mesopleural ridge not (primitive) or sharply (derived) carinate.

The derived state is found in most members of the Ticoplinae, Myrmillinae and Mutillini, and sporadically elsewhere, so that it shows many instances of parallel or convergent development. Intermediates also preclude unequivocal assignment of various members to one or the other state.

F59r. Meso-metapleural suture distinct (primitive) or obliterated and indistinguishable (derived).

Since the meso- and metapleura are fused in all members, there is a general tendency for the meso-metapleural suture to become obliterated, so that the derived state is expressed in many members independently in the various subfamilies and tribes involved. Furthermore, unequivocal categorization of the degree of distinctness

of the suture is impossible because of continuous variation from a quite distinct state to one in which the suture is completely indistinguishable.

F60r. Metapleural-propodeal suture distinct (primitive) or obliterated (derived).

As for character F59r, there is a general tendency for this suture to become obliterated so that the derived state shows many parallel and convergent occurrences, and also cannot be characterized unequivocally.

F61r. Calcar on front tibia with an elongate, narrow blade (primitive) or with a short, broad blade (derived).

Although all Mutillidae except Myrmosinae, Ticoptinae and Rhopalomutillinae tend to have the derived state, there is actually continuous variation so that definite decisions on which state is present are impossible in many instances.

F62r. Pectinal spines on fore tarsi barely developed (primitive) or highly elaborated (derived).

Although highly developed pectinal spines are mainly characteristic of many members of the Sphaerophthalminae and Mutillini, and also Pseudophotopsidinae, there is much variation within these groups so that it is impossible to decide unequivocally which state is involved in many cases. The derived condition has also arisen independently in various groups.

F63r. Mesotibia with two or more longitudinal rows of spines (primitive) or with only one or no rows of spines (derived).

Although degree of spininess is vaguely correlated with tribal groupings, the derived state has arisen on many independent occasions. There is also essentially continuous variation in the character so that meaningful states are impossible to define.

F64r. Metatibia with two or more longi-

tudinal rows of spines (primitive) or with one or no rows of spines (derived).

As with character F63r, the less spiny tibiae are mainly characteristic of some Sphaerophthalmini, Ephutini, Myrmillinae, Rhopalomutillinae and Ticoptinae, but extreme variability and impossibility of precise definition preclude the use of this character.

F65r. First metasomal segment sessile and not apically constricted (primitive) or petiolate, narrowed and apically constricted (derived).

Although the derived state tends to be restricted to various members of the Sphaerophthalminae, it has arisen on numerous occasions independently within the subfamily and is, furthermore, difficult to describe unequivocally since there is considerable variation in form. The derived state is also present in a less extreme form in many members of the Smicromyrmina.

F66r. First metasomal tergum extending over entire length of segment (primitive) or absent on anterior half of segment which is thus comprised of the sternum only (derived).

The derived state occurs in the Chyphotinae (Bradynobaenidae), so that with removal of this taxon from the Mutillidae, this character becomes invariant in the myrmosid-mutillid complex.

F67r. Second metasomal sternum without (primitive) or with (derived) a secretory felt line on each side.

The derived state occurs in scattered genera throughout the Mutillidae except for the Myrmosinae, Rhopalomutillinae, Sphaerophthalmini and Mutillinae, and thus may reflect a general tendency for the development of felt lines (whether tergal or sternal) in the Mutillidae (above the Myrmosinae), or may simply show numerous independent derivations.

F68r. Mesal stridulitrum on third meta-

somal tergum absent (primitive) or present (derived).

After removal of the Typhoctinae, Apterogyninae and Chyphotinae, this character is invariant in the myrmosid-mutillid complex, being present only in the derived state.

M69r. This character is the same as F44r, but for the male, and the same comments apply.

M70r. Head in anterior view tending to be vaguely triangular with the clypeal margin fairly short (primitive) or more rounded with the clypeal margin longer (derived) (see Fig. 80).

Although there is a striking difference in the shape of the head, the derived state being characteristic of all taxa except the Ticoplinae and less obviously the Myrmosinae and Pseudophotsidinae, and thus providing useful information establishing the holophyly of all Mutillidae above the three basal subfamilies, it is impossible to formulate the character states unequivocally so that they can be objectively applied.

M71r. Compound eye large (primitive) or small (derived).

Although this character is similar to F45r, and it was rejected for the same reasons, the distribution of the derived state is somewhat different. In the male small eyes occur in some Dasylabrini, most Sphaerophthalmini and most Myrmillinae.

M72r. This character is the same as F46r and the same comments apply.

M73r. Antennal scrobe dorsally unarmed (primitive) or with a tooth or transverse carina (derived).

Although the derived state tends to be present in most members of the Sphaerophthalminae, it also occurs sporadically in almost all the other subfamilies of Mutillidae. Unequivocal decisions on which

state is present are also often impossible, mainly because of the heavy sculpturing of many species.

M74r. This character is the same as F47r and the same comments apply.

M75r. This character is the same as F48r and the same comments apply.

M76r. First flagellar segment subequal to the second (primitive) or less than half the length of the second (derived).

The derived state is characteristic of most members of the Ticoplinae and also some Dasylabrini and a few Sphaerophthalmini and Mutillini, but cannot be unequivocally determined because of continuous variation between the two states.

M77r. This character is the same as F51r, but the derived state is more commonly present in the male, appearing in many members scattered throughout the Mutillidae.

M78r. Hind margin of pronotum shallowly arcuate (primitive) or deeply concave or angulate (derived).

Although the derived state tends to be characteristic of the Rhopalomutillinae, Myrmillinae and Mutillinae, scattered members of the other three higher subfamilies of Mutillidae also show it. The Myrmosinae have a more primitive condition than most other Mutillidae for this character. In addition, continuous variation precludes unequivocal decisions on which state is involved in many instances.

M79r. This character is the same as F53r and the same comments apply.

M80r. This character is the same as F54r and the same comments apply.

M81r. Mesoscutum with the parapsidal sutures and the parapsidal furrows both present (primitive) or with one (or both) of these paired "sutures" obliterated (various derived states).

Although most members show the

primitive state, some scattered members of the Sphaerophthalmini have lost the parapsidal sutures, as has *Smicromyrmilla*. The parapsidal furrows have been lost only rarely, e.g., in *Stenomutilla*. Both "sutures" are never lost simultaneously, it appears. Apart from the limitations caused by scattered occurrence, it is often difficult to ascertain the state, both because the degree of reduction of the "suture" varies and because it may be obscured by the sculpturing.

M82r. Axilla smoothly rounded posterolaterally (primitive) or produced into an obtuse or acute tooth (derived).

Although most members have the primitive state, various scattered genera, especially in the Sphaerophthalminae, show the derived state, which is furthermore difficult to designate unequivocally because of continuous variation.

M83r. Meso-metapleural suture fused for only a short distance ventrally (primitive) or fused for half its length or more (derived).

This character is associated with M27 in that only those members possessing state M27.1 have the meso-metapleural suture at all fused. This excludes the Myrmosinae, Pseudophotopsidinae and Ticoplinae from consideration. Most other mutillids possess the derived state of M83r, but various scattered members of the Sphaerophthalminae in particular have the primitive condition. Since there is also continuous variation it is impossible to designate the states unequivocally.

M84r. Metasternal process bidentate (primitive) or acute (derived).

This character is related to M28 in that it only applies to members possessing state M28.1. The Myrmosinae are thus excluded. The derived state of M84r has occurred on various occasions, being present in *Nanomutilla* (Ticoplinae), Rhopalomutillinae, some scattered Sphaeroph-

thalmini and Ephutini. Although the details of modification differ among the different groups involved, the differences are often subtle and difficult to designate unequivocally.

M85r. Metapleural-propodeal suture below the endophragmal pit not evident (primitive) or marked by a secondarily developed ridge (derived).

The primitive state is present in the Myrmosinae, Pseudophotopsidinae and Ticoplinae, and also in various scattered members of the Sphaerophthalminae, so that the derived condition must have arisen on numerous independent occasions. Because of essentially continuous variation and obscuration by sculpturing, unequivocal determination of the state represented is often impossible.

M86r. Tegula with inner margin approximately straight (primitive) or markedly concave as a result of posteromesal expansion of the tegula (derived).

Although most members possess the primitive state, a very few scattered genera (e.g., *Areotilla*, *Odontomutilla*, *Ctenotilla*, *Dolichomutilla*) show the derived state, the definition of which is also somewhat equivocal.

M87r. The forewing has three (primitive) or two (derived) or even one (further derived) submarginal cells (i.e., cell 2S or both 2S and 1S obliterated in the two derived states, respectively).

Many members scattered throughout the Mutillidae possess the first derived state (within some genera, e.g., *Dasylabris*, both the primitive and first derived states are found). Relatively few members possess the second derived state, but these are also scattered (e.g., *Ticopla*, *Atillum*). Thus both derived states have arisen on numerous independent occasions.

M88r. This character is the same as F61r and the same comments apply.

M89r. An arolium is distinctly present (primitive) or is absent (derived).

This character is comparable to F16 but shows a different distribution of states. After the removal of Typhoctinae, Chyphotinae and Apterogyninae, all members of the myrmosid-mutillid complex show the primitive state for character M89r. This character is thus invariant despite the fact that the females of Myrmosinae possess the comparable derived state (F16.I).

M90r. This character is the same as F65r except that in the primitive state the first metasomal segment is not as broad as in the female. Similar comments apply as to F65r, except that the derived state of M90r is present in the Rhopalomutillinae also. Furthermore, a different derived condition in which the first metasomal segment is apparently broadened seems characteristic of the Mutillina and to a lesser extent of the Ticoplinae and some Myrmillinae.

M91r. This character is the same as F66r and similar comments apply. It appears, however, that the derived state of this character is actually not present in the males of at least some Chyphotinae, but has been misinterpreted in the past.

M92r. Second metasomal sternum without (primitive) or with (derived) a secretory felt line on each side.

This character is the same as F67r but shows a different distribution in that the derived state is much more commonly present in the male, being found in scattered members of all taxa of the Mutillidae except for Myrmosinae, Rhopalomutillinae and Ephutini. (In addition some species of *Dasymutilla* and *Traumatomutilla* bear midventral felt lines on the second sternum.)

M93r. This character is the same as F68r and the same comments apply.

M94r. Hypopygium simple (primitive)

or with an upcurved aculeate spine (derived).

After removal of the Apterogyninae and Chyphotinae, all members of the myrmosid-mutillid complex possess the primitive state, although *Myrmosa* and *Rhopalomutilla* have the hypopygium modified in various ways.

M95r. Base of gonostylus approximately vertical (i.e., at right angles to longitudinal axis of genitalia) (primitive) or oblique (i.e., originating dorsally at a point more proximal than the ventral point of origin) (derived).

Although the derived condition is the more common, the primitive state occurs in the Pseudophotopsidinae and many scattered members of the Sphaerophthalminae so that there must have been numerous independent derivations. Also, because of continuous variation, unequivocal designation of the states is impossible.

M96r. Gonapophyses IX symmetrical (primitive) or with the right gonapophysis larger and more elaborate than the left (derived).

The derived state occurs in only a few members of the Smicromyrmina (viz., "*Lobotilla*," "*Timulla*," "*Trogaspidia*") and is thus only of use at the generic level.

## Discussion

### TAXONOMIC CONCLUSIONS

The final cladogram (Fig. 92) includes nine taxa, each of which is internally homogeneous for the various states of the particular characters considered (except for the few instances detailed in the above section describing these characters). As for the study of the Aculeata, values of *DF*, *DE*, *DC* and *DT* (various weighted measures of distinctness) were calculated (Tables IV and V). Although various characters occurring in both sexes were considered separately in cladogram con-



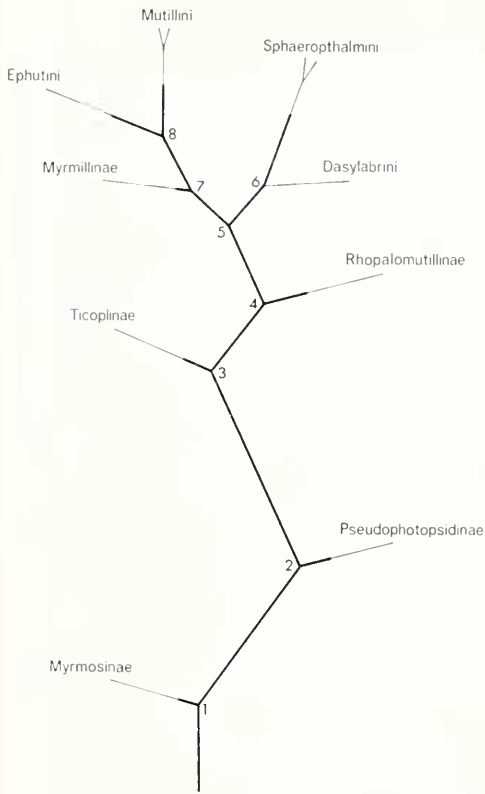


FIG. 92. Cladogram of nine taxa of Mutillidae; lengths of heavy lines are proportional to the distinctness measures (DC). Mutillini (comprising Mutillina and Smicromyrmina) + Ephutini = Mutillinae; Dasylabrini + Sphaerophthalmini (comprising Pseudomethocina and Sphaerophthalmina) = Sphaerophthalminae.

struction, they were combined and coded as to occurrence in the same fashion as for the aculeates for calculation of these values (i.e., a derived state occurring in only one sex on a particular internode was scored as 0.5 if it occurred in both sexes elsewhere on the tree). It should be noted that only the characters considered the most significant in deriving the cladogram have been included here, unlike for the Aculeata where all the characters considered were used. What influence this may have on the conclusions is unclear, although "poor" characters might be expected to occur at random on the tree and thus not affect the relative proportions of

"distinctness" for the various internodes. Certainly, the intuitive impressions gained during both investigations were supported by the values derived in each case.

The highest value for taxonomic distinctness (*DT*; Table V) between adjacent taxa is that for pseudophotopsidines and ticoplines, despite the fact that the myrmosines have commonly been excluded from the Mutillidae and so might be expected to show the greatest distinctness. The fact that the pseudophotopsidines are more distinct from the higher mutillids (minimum, 136) than from the myrmosines (108) strengthens the inclusion of the myrmosines in the Mutillidae. The ticoplines are also quite distinct from the rhopalomutillines (79) which in turn are slightly more distinct from the closest higher taxa (97 to myrmillines, 91 to dasylabrines). This suggests that the four basal taxa at least should each be recognized as distinct at the subfamily level. The myrmillines are somewhat less distinct from neighbouring taxa but approximately equally so (60 to both mutillines and dasylabrines). The two lowest values are those between the mutillines and ephutines (50) and the dasylabrines and sphaerophthalmines (37) indicating that these pairs should perhaps not be recognized at the subfamily level. The intermediate position of the myrmillines between two complexes which are highly distinct (minimum value 106, mutillines to dasylabrines) suggests that the three groups containing myrmillines, mutillines and dasylabrines each be recognized at the subfamily level.

The cladogram is thus interpreted to encompass one family, the Mutillidae, consisting of seven subfamilies, two of which comprise two tribes each. Two of these tribes (in different subfamilies) are in turn divided into two subtribes each, in both instances mainly on the basis of characters excluded in cladogram construc-

TABLE IV. Occurrences ( $\Sigma i$ ) and numbers (k) of derived states, number of species subtended (S) and various distinctness measures (DF, DE, DC) for the internodes and final branches of the cladogram of Mutillidae (Fig. 92).

Internode	$\Sigma i$	k	S <sup>a</sup>	DF	DE	DC
1-Myrmos.	3.0	4	50	11.04	0.83	9.16
1-2	5.0	5	4850	84.65	1.00	84.65
2-Psdpht.	5.0	5	50	18.40	0.80	14.72
2-3	7.0	7	4800	118.09	0.90	106.28
3-Ticopl.	4.0	4	75	16.88	0.88	14.85
3-4	3.0	3	4725	50.34	0.83	41.78
4-Rhopal.	7.0	7	50	25.76	0.86	22.15
4-5	3.0	3	4675	50.16	0.83	41.63
5-6	2.0	2	2475	27.06	1.00	27.06
6-Dasyla.	0.0	0	550	0.00	0.00	0.00
6-Sphaer.	3.0	3	1925	37.32	1.00	37.32
5-7	2.0	2	2200	26.00	1.00	26.00
7-Myrmil.	1.0	1	400	7.37	1.00	7.37
7-8	3.0	3	1800	36.48	0.83	30.28
8-Mutilln.	2.0	2	1500	22.90	1.00	22.90
8-Ephutn.	4.0	4	300	26.76	1.00	26.76

<sup>a</sup> Based on the sum of the estimated number of species in each genus (including those yet to be described). Calculations utilize  $\sqrt[3]{S}$ .

tion. The genera and subgenera included in these various taxa are listed in Table III.

**Mutillidae Latreille, 1802**

The Mutillidae as a whole is characterized by some quite strong synapomorphies, as outlined in the section on the Aculeata, above. The most significant of these are probably the development of a complex basal angulation of the scape, fusion of the moderately large prepectus to the mesepisternum, form of the modi-

fied mesosoma of the female (which is invariably apterous) and the development of a mesal stridulitrum on the third metasomal tergum.

Despite past attribution of the name Mutillidae to a wide variety of authors, it appears that Latreille's treatment was the first in which a group based on a genus included in this taxon was allocated a rank at the family group level.

**Myrmosinae Fox, 1894**

With the suite of characters in use here, the Myrmosinae has only five characters in the derived state, three of these being unique to this subfamily. In two there is parallel development of a derived condition in the Myrmosinae and also within the remaining Mutillidae, viz., unarmed claws and an unarmed mesosternum, both in the female only. Of the other three characters, the development of a dorsal lamella on the hind coxa in both sexes is probably the most significant. The remaining Mutillidae are distinguished from the Myrmosinae by the presence of six characters in the uniquely derived state. Of these, two involve the develop-

TABLE V. Taxonomic distinctness for the taxa of Mutillidae.

	MYRMOSINAE	PSEUDOPHTOPSIDINAE	TICOPLINAE	RHOPILOMUTILLINAE	DASYLABRINI	SPHAEROPHTALMINI	MYRMILLINAE	MUTILLINI	EPHUTINI
108									
215	136								
264	185	79							
310	231	125	91						
343	269	163	128	37					
317	233	132	97	60	98				
363	284	177	150	106	144	60			
366	287	181	154	110	147	64	50		

ment of an armed metasternum in both males and females, considered a single character for calculation of distinctness. The most useful character states uniting these higher taxa are the fusion of the pronotum with the mesothorax in the female and the form of the gonapophysis IX in the male. Although the absence of felt lines in the Myrmosinae has been considered to exclude them from the Mutillidae (e.g., Krombein, 1940), the development of felt lines in the higher subfamilies is somewhat irregular, so that this is not as fundamental a character as has been considered in the past.

The Myrmosinae is a relatively homogeneous group without any obvious subdivisions so that there does not seem to be any reason to subdivide it, at least not at this time. *Protomutilla* is perhaps the most anomalous member, and it may later be found that this genus is distinct enough to warrant the erection of a separate supra-generic taxon to contain it. Until the male is discovered, however, any such decision would be premature. Although Ghesquière (1951) placed the genera *Obenbergerella* Strand (= *Alienus* Bridwell) and *Alieniscus* Benoit as the tribe Obenbergerellini in the subfamily Myrmosinae of the Tiphiidae, Krombein (1957) included these genera in the Amiseginae, placed by him in the Chrysididae (Bethyloidea). Nagy (1969c) considered this group to fall in the Cleptidae. The females have 13-segmented antennae, only four exposed metasomal segments and only one spur on the hind tibia, among other characters. These characteristics exclude the group from the Myrmosinae but not from the Cleptidae or Chrysididae (*sensu lato*).

Handlirsch (1925) cites Ashmead (1896a) as the first to base a taxon of the family group on the genus *Myrmosa*. It appears, however, that Fox should be cited as the author since the paper in

which he established the tribe Myrmosini was published before that of Ashmead.

### **Pseudophotopsidinae** Bischoff, 1920

The Pseudophotopsidinae is distinguished from the higher Mutillidae (those above internode 2-3) by a relatively large number of characters. The most important of these are probably the retention of ocelli (or their rudiments) in the female in many species, retention of a distinct suture between the pronotum and mesonotum in the female, retention of a straight meso-metapleural suture in the male, retention of teeth on the claws in both sexes, retention of a jugal lobe in the hind wing of the male, retention of a rounded gonostylus in the male (all primitive states), development of a felted pronotal pit and mesosternal teeth in both sexes and development of articulating spines on the gonapophysis IX in the male in the Pseudophotopsidinae.

Although Schuster (1950) suggested that Krombein (1940) should be considered the author for this group, he apparently overlooked the fact that Bischoff, in his 1920-21 monograph, had based a tribe on the genus *Pseudophopsis*, in the section of that work published in 1920.

### **Ticoplinae** Nagy, 1970

The Ticoplinae differ from the higher groups of Mutillidae (i.e., those subtended by internode 3-4) by a number of characters, of which the following are probably the most significant: retention of setae and minute pores in the compound eye of both sexes, retention of an articulating meso-metapleural suture in the male (i.e., no development of a ventral bridgelike fusion) (both primitive characters although only the latter is shared with both the Myrmosinae and Pseudophotopsidinae), development of a posteriorly convex mesopleural margin in the male and development of a petiolate cell 1S in the forewing of the male. In addition the

form of the head (especially in the male) tends to be quite different from the other Mutillidae where the oral fossa appears to have been laterally expanded (less markedly so in the Pseudophotopsidinae, and barely so in the Myrmosinae, however). In general facies the females of the Ticoplinae appear to be more similar to the Myrmosinae than do any of the other higher Mutillidae. This is especially true of *Nanomutilla* which is uncannily similar to *Protomutilla*, whereas *Areotilla* is more similar to some species of *Myrmosa*. *Smicromyrmilla* is more highly modified in many respects and so shows less obvious similarity to the Myrmosinae.

In 1970 Nagy described the genus *Ticopla* (comprising two species) from two male specimens, both from the Jordan region. He made this genus the type of a new subfamily of his family Heterogynidae. (It appears that *Heterogyna* Nagy is actually a member of the Plumariidae—especially on the basis of wing venation—and it has been treated as such in the above investigation of the Aculeata.) Although it has been impossible for me to examine Nagy's specimens, it seems certain from his figure and description that *Ticopla* is very similar to *Nanomutilla*. *Ticopla* has the wing venation more reduced, however, and the genitalia may be somewhat different although Nagy's description of these is not detailed enough for certainty. In particular, these genera are similar in various characteristics cited by Nagy as indicating relationships of *Ticopla* to the Bethyliidae rather than the Mutillidae, such as the position of the compound eye (very short malar space), setae on the eye, acute posterolateral angle and pattern of sculpturing of the propodeum, and the prominent setae on the major wing veins. It thus seems that *Ticopla* is in actual fact a member of the Mutillidae, closely related to *Nanomutilla*. On this basis, the subfamily including

*Nanomutilla* (and thus *Ticopla*) must be designated the Ticoplinae since Nagy has already based the name of a taxon of the family group on that genus. It may even be that a species of *Ticopla* is actually the male of *Nanomutilla vaucheri* (Tournier), females of which have been collected in the same region (André, 1902). If this should prove to be true, then *Ticopla* would have to be synonymized with *Nanomutilla*, although the subfamily name would be unchanged.

Within the Ticoplinae there are no particularly marked groupings (other than that of *Nanomutilla* and *Ticopla* already mentioned), so that tribal divisions are unwarranted. The most distinct genus is probably *Smicromyrmilla* which possesses sternal felt lines as well as a variously armed mesosoma. The female in particular has a superficial similarity to some members of the Myrmillinae, especially in mesosomal form, as has been noted by Suárez (1965). The males of *Smicromyrmilla* also show a complete gradation from fully winged forms to species without any trace of sutures on the mesosomal dorsum, a condition found elsewhere only in *Brachymutilla* (Dasylabrini). Nevertheless, the least-modified members (especially the males) are reasonably similar to *Nanomutilla* and were placed in this genus by Bischoff (1920-21). This placement may, however, have been due in considerable part to the fact that Bischoff had seen neither the type species (*N. vaucheri*) nor the only other species placed in *Nanomutilla* by André (the author of the genus) up to that time, but apparently based his generic allocation mainly on the presence of a petiolate cell 1S, which is now seen to be a subfamily characteristic. Although Nonveiller (1973) recognized the confusion then existing between *Nanomutilla* and *Smicromyrmilla*, he had apparently not seen any male specimens of *Nanomutilla*.

**Rhopalomutillinae** Schuster, 1949

The Rhopalomutillinae differ from the higher Mutillidae (i.e., those subtended by internode 4-5) in the retention of a relatively long pronotum in the female, the absence of any felt lines and the retention of a small metacoxal tubercle in both sexes (all primitive states) and from all other members of the family in the reduced maxillary and labial palpi of the female, the form of the mesosoma and first metasomal segment in the female (although a somewhat similar but less extreme development of the metasoma has occurred in the Sphaerophthalmini in the complex of species related to "*Ephutomorpha*" *addenda*), and the development of a basal lamella on the tarsal claws in the male. In addition, the hypopygium of the male is much modified, being reduced and often with complex protuberances, a condition unlike that in other Mutillidae (the hypopygium is also reduced but differently modified in many Myrmosinae).

Although Schuster in 1947 considered *Rhopalomutilla* to be of doubtful position, in or near the Sphaerophthalminae, he did not designate any family level group to contain it at that time. However, in his 1949 treatment, Schuster used the term "Pseudophotopsidinae-Sphaerophthalminae-Mutillinae-Rhopalomutillinae complex" when referring to the taxon here considered to comprise the Mutillidae (except for the Myrmosinae). He also gave a few characters (pp. 123, 125) differentiating the Rhopalomutillinae from other groups. This is apparently the first instance in which a family level group name was based on *Rhopalomutilla*.

**Sphaerophthalminae** Schuster, 1949 (1903)

The Sphaerophthalminae differ from the two higher subfamilies (subtended by internode 5-7) in their retention of a completely sclerotized pterostigma and also in the form of the mesosoma in the

female and the direction of curvature of the gonostylus in the male.

In his classification of the Mutillidae, Ashmead (1903-4) based two tribes on genera which are included in the present concept of the Sphaerophthalminae. These were the Photopsidini (in his subfamily Mutillinae) and the Sphaerophthalmini (sic) (in his Ephutinae). Although the name "Photopsidinae" was used by Bradley & Bequaert (1928) and by Schuster in the first paragraph of his 1947 paper, Schuster in the same paper later specifically designated this group as the Sphaerophthalminae (sic), because "*Photopsis* is not generically distinct from *Sphaerophthalma*" (sic). [The confusion in the spelling of the generic name has arisen because Blake's (1871) original spelling, *Sphaerophthalma*, was an incorrect transliteration from the Greek—*σφαίρα* a ball, and *οφθαλμος* an eye—which Blake corrected in 1886 to *Sphaerophthalma*. This corrected spelling was used uniformly from then on until Schuster (1949) reverted to the original spelling as the basis for the name "Sphaerophthalminae." The "corrected" (1886) form is an unjustified emendation under the provisions of Articles 32(a) & 33(a) of the International Code of Zoological Nomenclature (1964), since Blake's change was obviously intentional, appearing consistently in many places in his 1886 paper. As such, *Sphaerophthalma* Blake, 1886 must be considered a junior objective synonym of *Sphaerophthalma* Blake, 1871, rather than merely a misspelling.] This change in the name has won general acceptance and was used by Krombein (1951) in his catalog of the Mutillidae of America North of Mexico, with the additional change of spelling resulting from Schuster's (1949) correction of the spelling of the type genus. The appropriate name to be conserved under Article 40 of the International Code of Zoological Nomenclature

(1964) is thus "Sphaerophthalminae," which is considered to date from 1903 when it was in effect first used by Ashmead. (The citation of author and date, as in the heading to this section, follows Recommendation 40A of the Code.)

#### Dasylabrini Invrea, 1964

The Sphaerophthalminae contains two distinct groups, one of which (Sphaerophthalmini) is recognized by a few quite distinct derived states. The Dasylabrini, however, does not possess any particular derived characteristics which would indicate it as a holophyletic group. It may thus be that it is actually paraphyletic, representing those members of the Sphaerophthalminae which do not fall in the holophyletic tribe Sphaerophthalmini. Since homogeneous paraphyletic groups fulfill the criteria of monophyly generally required of named taxa (Tuomikoski, 1967; Ashlock, 1971), recognition of the Dasylabrini as a named taxon is not illegitimate. Within the Dasylabrini there are no particular subgroups recognizable, so that the entire taxon is best regarded as a single tribe. Although Skorikov (1935) seems to have been the first to propose a family level group name based on one of the genera (*Dasylabris*) included here, he did not characterize the group. Apparently Invrea (1964) was the first to fulfill all the requirements of the International Code of Zoological Nomenclature (1964).

#### Sphaerophthalmini Schuster, 1949 (1903)

The tribe Sphaerophthalmini is distinguished from other members of the subfamily by some unique derived states in both sexes. These are the form of the eye which is approximately hemispherical and often smooth and polished (particularly in the male) and the development of plumose pubescence. These characteristics unite a large and varied group of genera which Schuster (1947) considered to comprise at least five taxa, each apparently at

the tribal level, although this was not explicitly stated. In 1958 Schuster revised one of these groups and Krombein (1967) designated it a tribe, so that his "Sphaerophthalmini" is more restricted than the group included here under that name.

When the members of the Sphaerophthalmini were examined more closely, using many of the characters which were rejected for the study as a whole, no very distinct groupings were recognizable. The most distinct subgroup is that including *Pseudomethoca* and related taxa, mainly based on the form of the female mesosoma and the tendency for both sexes to have the metasoma sessile. The remaining members are associated by a tendency toward development of a petiolate metasoma in the male and sometimes in the female, but do not fall into any further clear subgroups. There is instead a continuum from those genera with fewest derived states to those with many. Although no final decisions can now be made on the evolutionary relationships among these genera, since additional investigations and clarification of generic limits are needed, it is nevertheless clear that the genera nearest the base of the line are those like *Cystomutilla*, *Photomorphus* and *Protophopsis*, with the moderately advanced ones being similar to *Sphaerophthalma*, *Lomachaeta* and *Dasymutilla*, and the most highly derived ones being some members of the "*Ephutomorpha* complex," such as *Ascetotilla* and the group of "*Ephutomorpha*" *paradisiaca*.

At this point it seems best to consider the tribe Sphaerophthalmini to consist of two more or less equal subdivisions which may be given the status of subtribes. The group with a generally sessile metasoma is the **Pseudomethocina**. [Although Schuster (1947) characterized this group, he referred to it as the "Pseudomethocine complex." Suárez (1962) was apparently the first to Latinize the name (as Pseudo-

methocini), but he did not accompany it with any differentiating characters, nor has this been done since. It thus seems that the name should formally be considered to date from the present paper.] The group with the metasoma tending to be petiolate (in the male at least) is the **Sphaerophthalmina** Schuster, 1949 (1903). Additional and more detailed investigations of this tribe may quite likely indicate that fewer or more such subtribal divisions are warranted.

#### Myrmillinae Bischoff, 1920

The Myrmillinae differ from the Mutillinae in the retention of a simple, short tegula and broadly oval eye with shallowly sinuate inner margin in the male (both primitive states) and also in the form of the pterostigma in the male. The form of the mesosoma in the female is also different, with the pleura in the Myrmillinae tending to be evenly concave and rather smooth (except that the mesopleural ridge tends to form a strong carina or lamella ventrally just anterodorsal to the mid-coxa), and the pronotal-mesopleural suture is essentially obliterated. Female Myrmillinae also tend to have the head rather heavy, often roughly quadrate with the gena somewhat swollen and with the mandible very strong and broad apically. Although the females of Myrmillinae are sometimes difficult to allocate unequivocally to this subfamily without prior experience, having few good features to distinguish them from Mutillini, the males are quite distinct.

Since this family is confined to the Old World, its members were apparently not included by Schuster (1947) in his general scheme. Interestingly, Skorikov (1927, 1935) placed this subfamily in the Myrmosidae. Bischoff (1920-21), apparently the first to base the name of a group at the family level on that of one of the genera included here in the Myr-

millinae, derived the myrmillines as a separate branch from a myrmosid ancestor but included them in his Mutillinae and not the Myrmosinae!

Within the Myrmillinae there are no definite subgroups of genera which could be designated as tribes. It is of some interest that this subfamily includes the highest proportion of species with brachypterous or apterous males of all the subfamilies. Various genera contain both fully winged and wingless species (e.g., *Myrmilla*, *Labidomilla*) although the range of variation in these is not as great as in *Smicromyrmilla* (Ticopliinae) where the most advanced forms have in addition lost all traces of sutures dorsally on the mesosoma.

#### Mutillinae Latreille, 1802

The Mutillinae is characterized by development in the male of a posteriorly produced tegula, deeply and sharply emarginate eye and a completely membranous pterostigma. (The pterostigma is further entirely lost in some members.)

#### Mutillini Latreille, 1802

This tribe is distinguished by the development of a recurved posterior margin of the tegula in almost all genera and, in the female, by the dorsal depression of the mesopleural ridge and modifications of the meso-metapleural suture (except for *Odontomutilla*).

The tribe Mutillini itself consists of a large number of genera which fall into two reasonably distinct groups. The smaller group consists of a few genera with males which tend to have the mesosoma somewhat compact and the metasoma completely sessile, with the first tergum somewhat broadened. The females also have the first metasomal tergum broadened and often almost disclike. This group may be designated the subtribe **Mutillina** Latreille, 1802. The other, larger, group has males which are gen-

erally slightly more slender, with the first metasomal tergum almost campaniform, narrower and weakly demarcated from the second. The females also have the first metasomal segment narrower and sometimes almost petiolate. This second group is the subtribe **Smicromyrmina** Bischoff, 1920. Actually this subtribe includes two of Bischoff's (1920-21) tribes, his Smicromyrmini and Trogaspidiini. In contrast to Bischoff's treatment, Bradley & Bequaert (1923) placed many of the genera included in both "tribes" under the genus *Smicromyrme*. Mickel (1933) once more considered *Smicromyrme* and *Trogaspidia* to be generically distinct (although he placed the latter as a subgenus of *Timulla*). Since that time various authors of major works have treated *Trogaspidia* either as a subgenus of *Timulla* (e.g., Mickel, 1935; Krombein, 1971) or as a distinct genus (e.g., Olsoufieff, 1938; Chen, 1957). Furthermore, Krombein (1972) returned to Bischoff's (1920-21) concepts of tribal classification, but changed the name of the Trogaspidiini to the Timullini (a procedure disallowed under Article 40 of the International Code of Zoological Nomenclature, 1964). In view of the confusion surrounding the name *Trogaspidia* it thus seems best to use *Smicromyrme* (which is also the older name) as the type genus for this subtribe.

#### **Ephutini** Ashmead, 1903

The Ephutini is a very distinct group, characterized by the peculiar cylindrical form of the first metasomal segment in both sexes, the form of the mesosoma in the female and the tegula in the male, as well as the loss of the pterostigma.

There are no distinct subgroups within this tribe so that no subdivisions can be recognized, although much work needs to be done to clarify generic limits. It appears that Ashmead (1903-4) was the first to base a family-level name on the genus

*Ephuta*, first doing so adequately in the section of his paper published in 1903.

The morphological investigation thus indicates that the family Mutillidae may be considered to be composed of seven subfamilies, five of these being monotypic; the other two subfamilies each contain two tribes and, in each, one of the tribes comprises two subtribes. This arrangement should be found to be useful and stable provided that it is based on an accurate interpretation of the patterns of evolution within the family. Some indication of the probable accuracy of a cladogram may often be obtained when external data are superimposed on it and their fit to the scheme is judged. Such data may be biological (information on life histories, hosts, etc.) or distributional, and these two types of data will be evaluated below.

#### LIFE HISTORIES AND HOST RELATIONSHIPS

Unfortunately, rather little work has been done on the life histories of the Mutillidae. Detailed, although nevertheless incomplete, information is available for *Chrestomutilla glossinae* (Lamborn, 1915, 1916; Heaversedge, 1968, 1969a & b, 1970) (Dasylabrini), *Dasymutilla bioculata* (Mickel, 1924; Cottrell, in Brothers, 1972) and *Sphaerophthalma (Photopsis)* spp. (Ferguson, 1962) (Sphaerophthalmina), and *Pseudomethoca frigida* (Brothers, 1972) (Pseudomethocina) in the Sphaerophthalminae, and also for *Smicromyrme rufipes* (Crèvecoeur, 1930; Maréchal, 1930) (Smicromyrmina) and *Mutilla europaea* (Hoffer, 1886; Jordan, 1935; Pouvreau, 1973) (Mutillina) in the Mutillini. Reasonably detailed information also exists for *Myrmosula parvula* in the Myrmosiinae, although this is as yet unpublished (Brothers, in prep.). There are only brief observations on mating, feeding and other details for the subfamilies Pseudophotopsidinae, Rhopalomutillinae and Myrmilli-



nae, as well as the Ephutini. There is essentially no information on the Ticoplineae.

In view of the paucity of data, it is impossible to ascertain whether life history information supports the cladogram or not. The time and method involved in mating seem to differ according to taxonomic unit. Sphaerophthalmini such as *Dasymutilla* (Cottrell, in Brothers, 1972; Linsley, MacSwain & Smith, 1955), *Photopsis* (Ferguson, 1962; Salman, in Mickel, 1938) and *Pseudomethoca* (Brothers, 1972) mate on the substrate, intromission lasting a few seconds. The males of Smicromyrmina (Mutillini) such as *Timulla* (Linsley, 1960; Sheldon, 1970), *Smicromyrme* (Bertkau, 1884; Crèvecoeur, 1930; Pagden, 1934) and *Sulcotilla* [specimens in British Museum (Natural History) collected by Risbec] often transport the female in flight before settling and mating. They may even mate in flight, the male clasping the female with his mandibles and legs. In the Rhopalomutillinae also, the male transports the female (Bridwell, 1917; Pagden, 1938), but in this case the female is supported entirely by the attachment of the male genitalia and by modifications of the apical sterna of the male. In *Rhopalomutilla tongana* at least, the relative positions of the male and female are similar to those figured by Evans (1969a) for *Apenesia* (Bethylidae) (and thus unlike most Thynninae), although the size difference between the sexes is greater in *Rhopalomutilla* (pers. obs.). In the instance observed, the male was visiting the flowers of *Zizyphus* with the female attached passively to his metasomal apex. In some Myrmosinae, also, the male transports the female during copulation, with the female below the male and venter to venter, the only support of the female being provided by the genitalia of the male (*Myrmosa*; Townes, in Pate, 1947a; Krombein, 1956). It is obvious that phoretic copulation is most likely to occur

in species where the male is appreciably larger and stronger than the female. This condition occurs most markedly in the Rhopalomutillinae, many but not all Smicromyrmina and some Myrmosinae, as well as some species in other groups. Thus, information on mating may elucidate phyletic relationships within the higher groups but will probably not be particularly useful in confirming (or refuting) the present cladogram based on adult morphology.

Other biological data which have been found to be useful in other parasitic groups, are host relationships. If the parasites tend to be at all host specific, they should show a pattern of evolution which is compatible with that of the host organisms, unless there have been transfers to unrelated hosts. Such data have, for example, proved to be useful in studies of mammalian ectoparasites (see Traub, 1972, for a discussion of the interrelationships of evolutionary patterns and geographic distributions of fleas and mammals). From the available host records, it appears that no parallels can be drawn between the evolution of the Mutillidae and that of their hosts. Members of this family were almost certainly originally parasitoids of ground-nesting Hymenoptera, as are the Fedtschenkiinae (Bohart & Schuster, 1972). However, host specificity is apparently often not strict [e.g., *Stenomutilla argentata* parasitizes Eumenidae (Vespoidea), Megachilidae (Sphecoidea) and Clytrinae (Coleoptera; Chrysomelidae) (Giner Marí, 1944); *Pseudomethoca frigida* attacks at least eight species of halictine bee and perhaps a eumenid wasp (Brothers, 1972)], and transfers to entirely unrelated hosts (even in different orders) have apparently occurred sporadically. Thus, Coleoptera and Diptera are utilized by a few members of the Dasylabrini and Smicromyrmina, Lepidoptera only by *Stenomutilla* (Dasylabrini) and

at least some *Odontophotopsis* may parasitize cockroach oothecae (Mickel, 1928, 1974; Seyrig, 1936). As a result, it appears that host information is of no use in confirming or refuting the cladogram. Instead, members of the Mutillidae seem to be capable of parasitizing a wide variety of hosts, the one requirement perhaps being that the stage of the host attacked be in the form of a more or less immobile "package" sealed off from the environment, whether in a closed cell or a hard cocoon, puparium or ootheca.

#### GEOGRAPHIC DISTRIBUTION

Since the Mutillidae comprises exclusively species with low vagility as a result of the winglessness of the females, it might be expected that the geographic distributions of the various subtaxa would reflect their places (and times) of origin when considered in the light of the theory of plate tectonics and continental drift, if the group is of appropriate age. This should be more clearcut than for a group with high vagility which could more easily cross water gaps. In fact it appears that the cladogram of the Mutillidae is consistent with the data on geographic distribution, and is thus supported (or at least not refuted) by it. The distribution of the more primitive subfamily (Fedtschenkiinae) of the sister group to the Mutillidae (the Sapygidae) is also of importance in this regard, since it provides a clue as to the area in which the ancestor of the Mutillidae arose. [The more derived Sapyginae are essentially cosmopolitan—absent only from the Australian region (Pate, 1947c)—and thus do not provide any useful data.] Although the cladogram is not being used here as evidence for former land connections, as was the purpose of Hennig (1966b) in his survey of the Diptera fauna of New Zealand, the rigorous principles which he outlined in that paper still apply.

Reconstructions of Pangaea and the sequence of events leading to fragmentation and rearrangement of the components, together with estimates of the times involved, have been attempted by various authors and are being steadily refined. The following sequence has been derived from information presented by Dietz & Holden (1970), Axelrod & Raven (1972), Fooden (1972), Raven & Axelrod (1972) and Heitzler *et al.* (1973). Most of these authors have based their concepts on data derived from a wide variety of sources, in large part geophysical. This sequence should, nevertheless, be regarded merely as the best estimate derivable from their data.

About 200 million years (m.y.) ago (during the Triassic) there was apparently a single land mass, Pangaea, surrounded by the universal ocean, Panthalassa, an arm of which formed the Tethys Sea separating Eurasia and Africa. The first rift occurred in the west and separated North America from South America and Africa, resulting in two continental areas, Laurasia and Gondwana, with tenuous contact maintained across the Gibraltar area (180 m.y., late Triassic—early Jurassic). About 150 m.y. ago (middle Jurassic), the Indian Ocean first opened from the east, separating East Gondwana (consisting of Australia-New Guinea, New Zealand and Antarctica) from West Gondwana (India, Madagascar, Africa and South America) although contact was maintained between Antarctica and South America. The next rift occurred within West Gondwana when South America split off from Africa (110 m.y., mid-Cretaceous), although these two continents remained reasonably close to each other for perhaps another 20 m.y. because their relative movement in the north resulted from a shear fault (similar to the San Andreas Fault in California). The next separation was that of New Zealand from

West Antarctica (80 m.y., late Cretaceous), thus splitting East Gondwana. Shortly thereafter (70 m.y.) India separated from Africa and Madagascar and began its migration north-eastward. About 60 m.y. ago (late Cretaceous—Paleocene) Madagascar split off from Africa and, as a result of rotational movements, the Arabian section of the African plate came into contact with Eurasia, cutting off the Mediterranean Sea from the western extremity of the Tethys. Not long after this (50 m.y., Eocene) North America and Greenland finally separated from Europe, although this rift had gradually been extending northwards since its initiation more than 80 million years before. At about the same time, Australia-New Guinea split off from East Antarctica and moved northward, contacting the eastern region of the Asian plate about 20 m.y. ago (Miocene). India collided with Asia about 15 m.y. ago and North and South America were linked only about 10 m.y. ago (early Pliocene). In addition, Antarctica only moved to its polar position within the last 40 m.y., after Australia had separated from it, its climate up to that time having been much milder than presently. Also, New Caledonia remained linked to (or at least close to) Australia for a short time after New Zealand had separated from the rest of East Gondwana.

The present disjunct Holarctic distribution of *Fedtschenkia* (Fig. 93; Guiglia, 1972) probably represents the relicts of a more widespread group which was undoubtedly of Laurasian origin. (The Sapyginae have apparently radiated from this area, perhaps relatively recently since they are not found in the Australian region.) The Myrmosinae (Fig. 94) are also confined to the Holarctic region although the single modern representative of the derived genus *Protomutilla* occurs in the Oriental region. Fossil specimens of *Protomutilla* are, however, from Baltic

amber (Bischoff, 1915), so that members of this group were probably present throughout Eurasia. Apparently both the Fedtschenkiinae and the Myrmosinae originated on Laurasia and dispersed throughout this area after the splitting of Pangaea into Laurasia and Gondwana. Even after this break, however, there was still contact (at least intermittently) across the region of Gibraltar, which may explain the presence of *Myrmosa* in North Africa (although this is perhaps more likely a later development).

By contrast, the Pseudophotopsidinae (Fig. 95) is presently distributed across the northern section of Africa, Arabia and into southwestern Asia. The Ticopliinae (Fig. 96) is predominantly African although apparently absent from the Saharan area (perhaps a secondary development because of ecological changes), and also occurs in India and Spain. The Rhopalomutillinae (Fig. 97) is again mainly tropical African but with representatives in the Oriental region.

Since these three are the most basal groups of Mutillidae (apart from the Myrmosinae), it seems that the center of origin for this section of the family was the African plate, and probably its northern section. This likely resulted from the introduction of an ancestral form across the Gibraltar region at about the time that the final break occurred between Laurasia and Gondwana. The ancestral form gave rise to the Pseudophotopsidinae which apparently spread to the east and eventually across the Arabian area and on to the Eurasian plate after contact was reestablished there. The most generalized species of *Pseudophotopsis* is probably *P. continua* (ocelli and dorsal mesosomal sutures in the female the least reduced) which is widespread in North Africa. The more eastern species are generally more highly derived (e.g., *P. syriaca*), which supports this pattern of dispersal.

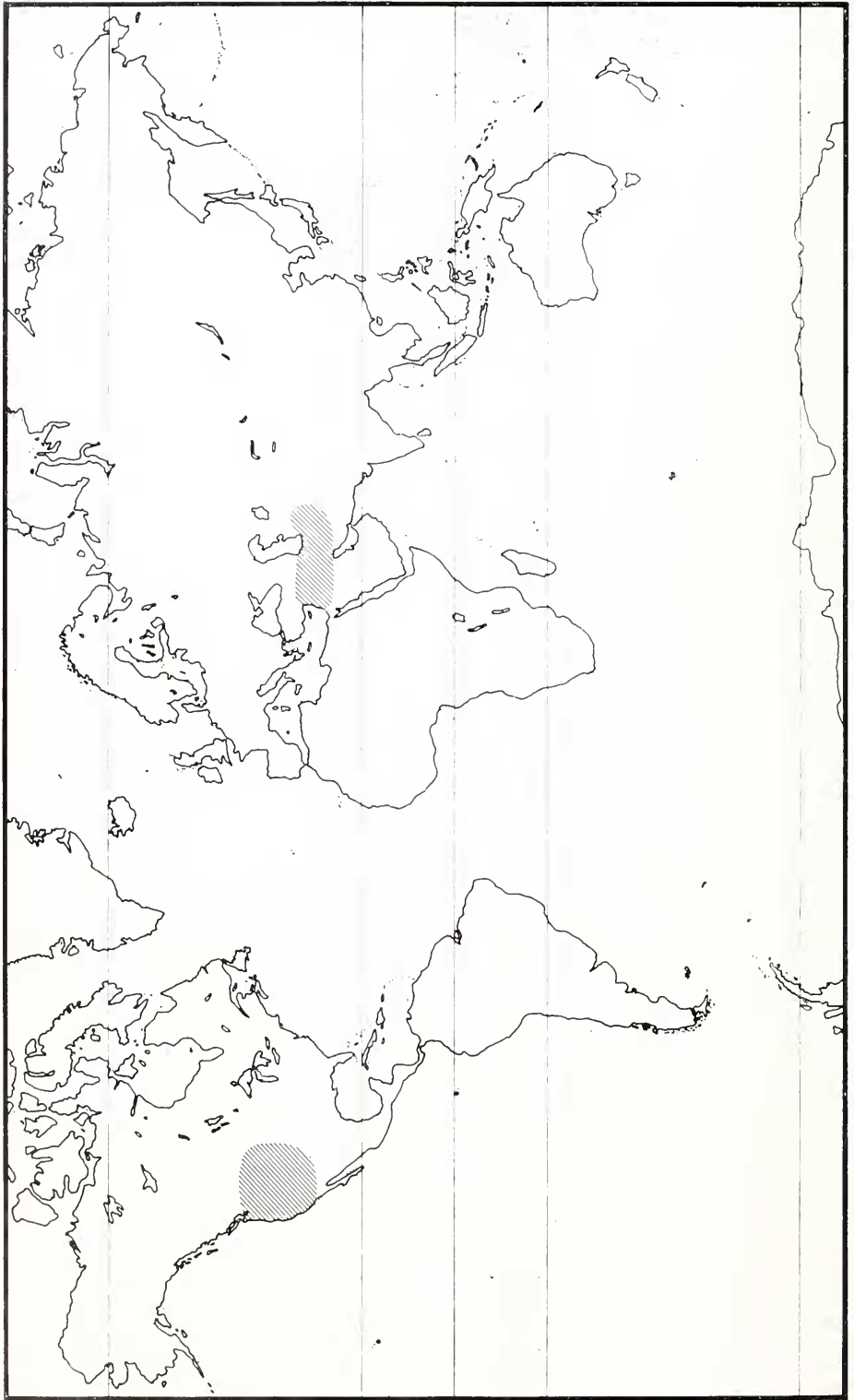


FIG. 93. Geographic distribution of Fedtschenkiinae (Sapygidae).

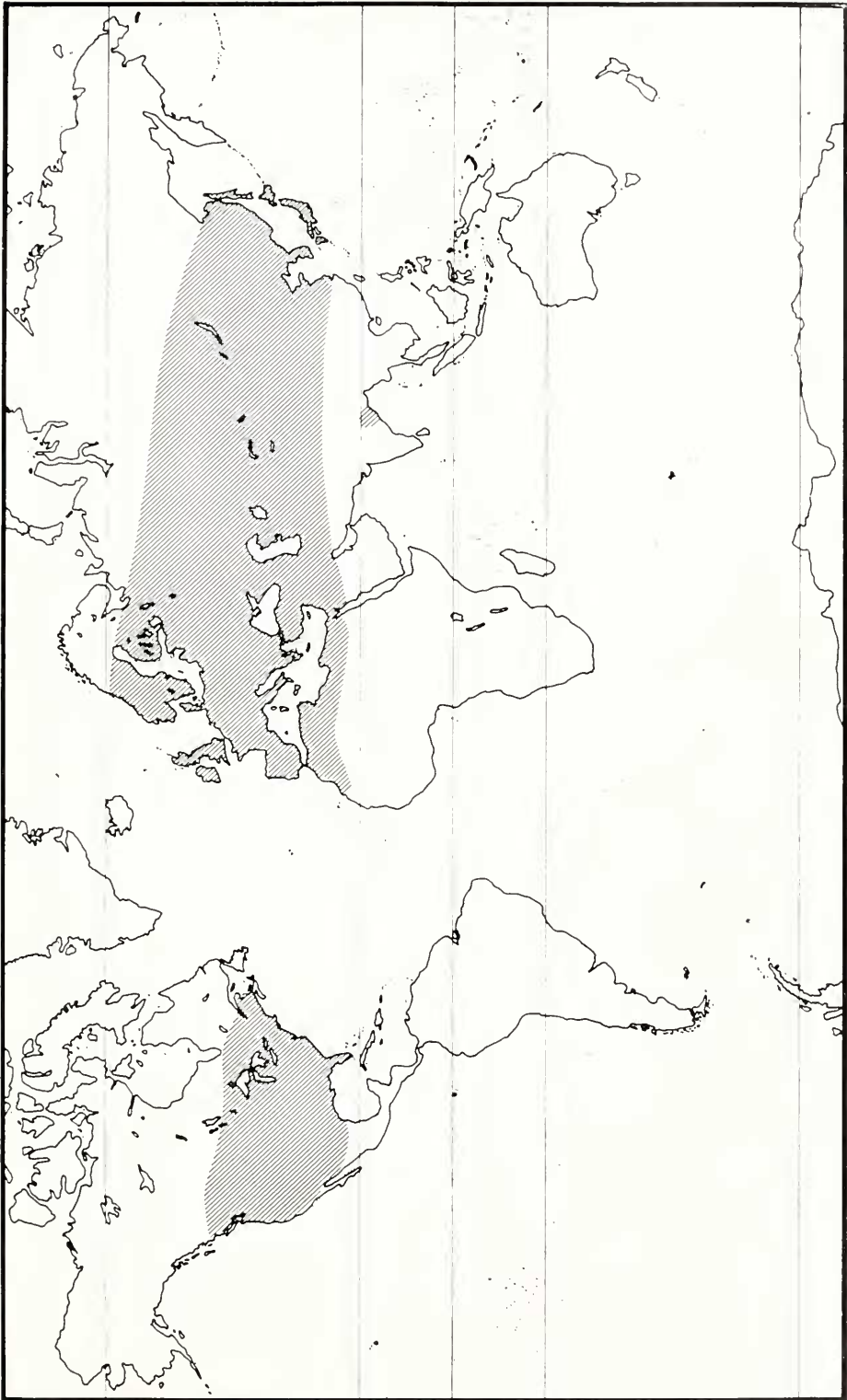
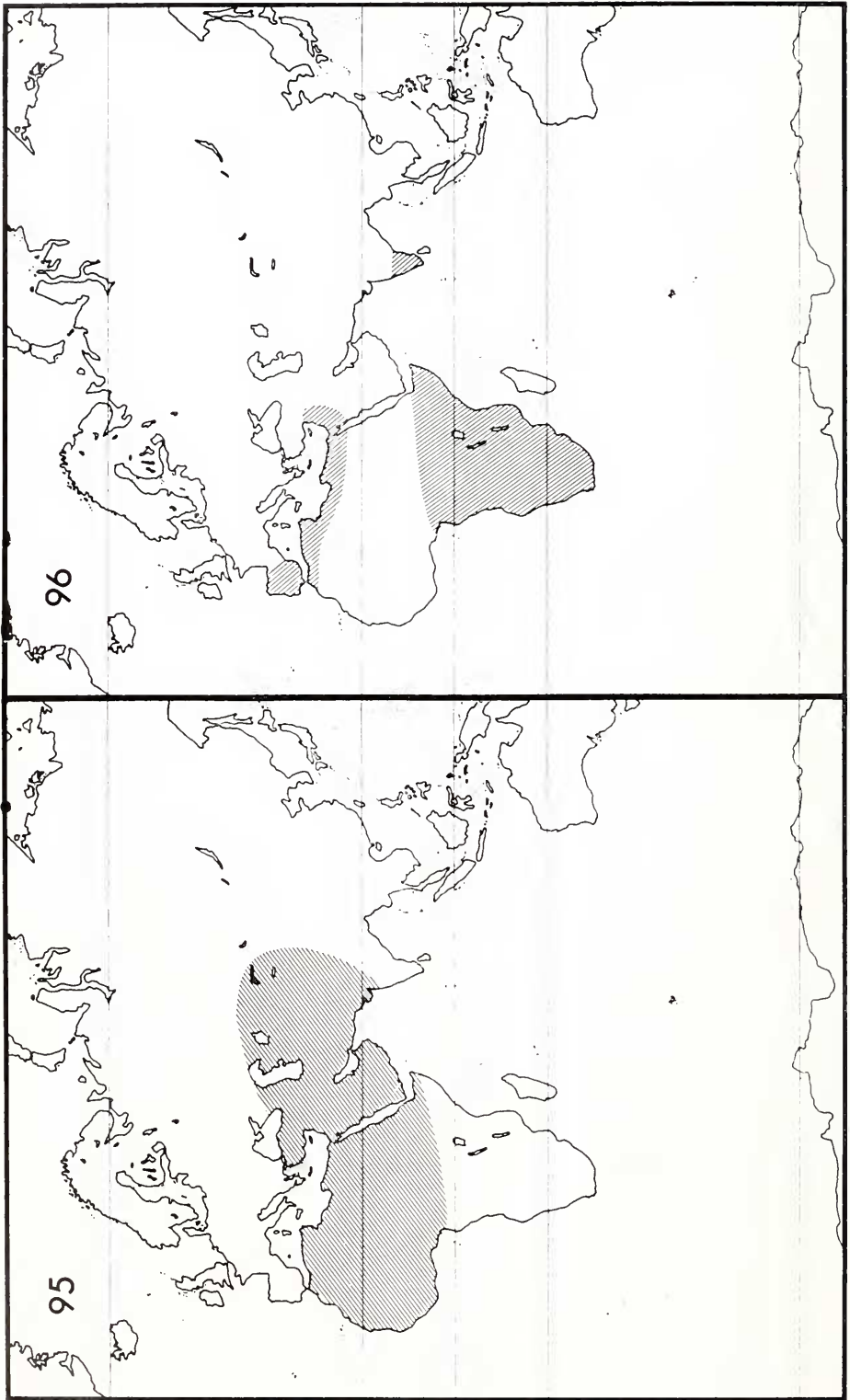
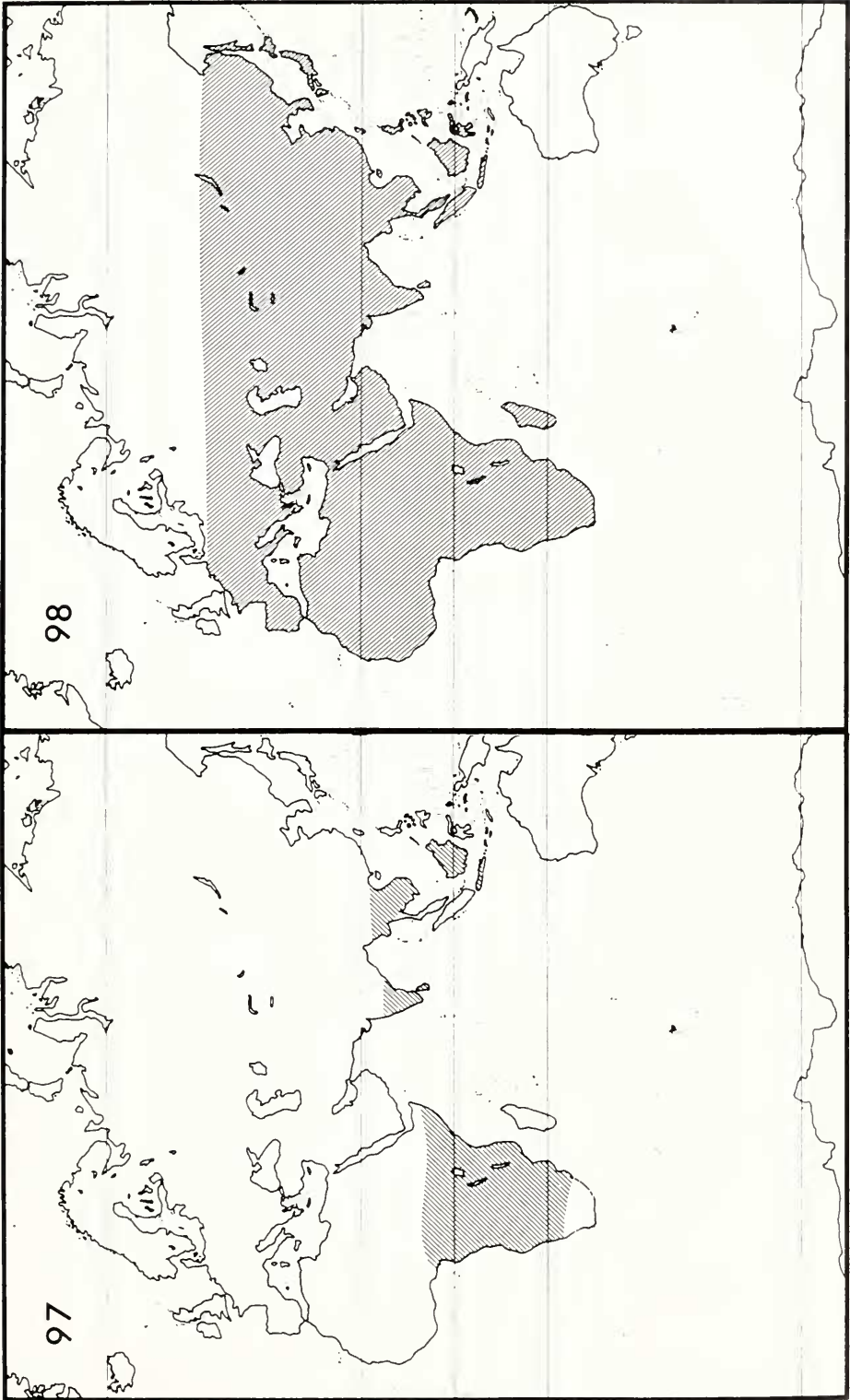


FIG. 94. Geographic distribution of Myrmosinae (Mutillidae).



Figs. 95-96. Geographic distribution of subfamilies of Mutilidae. 95, Pseudophotopsidinae; 96, Ticoplinae.



Figs. 97-98. Geographic distribution of subfamilies of Mutilidae. 97, Rhopalomutillinae; 98, Myrmillinae.

The ancestral Ticoplinae probably arose somewhat farther south and east on the African plate. This group then may have diversified and spread on to the Indian plate while it was still in contact with Africa or at least close to it. At least one member apparently crossed the Gibraltar area to Europe, probably much more recently. Although it is difficult to state which genus of Ticoplinae is the most generalized, it seems clear that the most specialized morphologically is *Smicromyrmilla*, which is also the most widespread at present, and the one which occurs in both Spain and India, as well as Africa. (Some Indian species have the most highly derived males of the subfamily since they are completely apterous and lack any traces of sutures on the mesosomal dorsum.) This is not inconsistent with the concept of diversification of the group from an African center.

A similar sequence may have led to the origin of the Rhopalomutillinae, which seem to be adapted to more tropical conditions than the Ticoplinae. Rhopalomutillinae also probably spread from the African to the Indian plates, and when India came into contact with the Eurasian plate there was apparently additional diversification and dispersal of this subfamily to the east into Indo-China and further to Borneo and Java. From morphological considerations it appears that the most generalized species of *Rhopalomutilla* occur in Africa (e.g., *R. tongaana*; least modified hypopygium in the male) and some of the more highly derived are the Asian species (e.g., *R. oceanica*), a distribution not inconsistent with the above ideas.

These three basal subfamilies were probably confined to the east African region, at least initially, since none of them occurs in the New World. This may have resulted from the presence of epicontinental seas over much of northern and

western Africa during the Cretaceous (Cracraft, 1973). The absence of the Ticoplinae and Rhopalomutillinae in Madagascar is somewhat puzzling and requires further elucidation. These groups may, however, have become extinct there, perhaps as a result of competition from the more advanced subfamilies. Until more data have been gathered on these groups, further speculation is pointless.

The subfamily Sphaerophthalminae is cosmopolitan in distribution (Fig. 99). However, the more generalized tribe (Dasylabrini) is confined to the Ethiopian, southern Palearctic and Oriental regions (with one species of *Stenomutilla* on the Solomons in the Australasian region). The most widespread genera are *Dasylabris* and *Stenomutilla*, both of which extend over approximately the entire range of the subfamily. The most derived genera are probably *Apteromutilla* and *Brachymutilla* (both with apterous males), both of which are confined to the southern tip of Africa. This distribution is not inconsistent with an origin for the group in north-eastern Africa with the spread of two vigorous genera into Eurasia, either across Arabia when contact was established there or by transport on the Indian plate, or both. Diversification and dispersal also apparently occurred toward the south and west across Africa.

The tribe Sphaerophthalmini (Fig. 99) occurs entirely in the New World and the Australasian region, apart from the genus *Cystomutilla* (two species) which now occurs in the Mediterranean region and Japan, a somewhat enigmatic situation. Except for *Cystomutilla* (which may actually be misclassified as a result of parallel development of certain characters), this distribution may have resulted from a single introduction of an ancestral sphaerophthalmine from Africa into South America at about the time that these two continents separated. After becoming es-



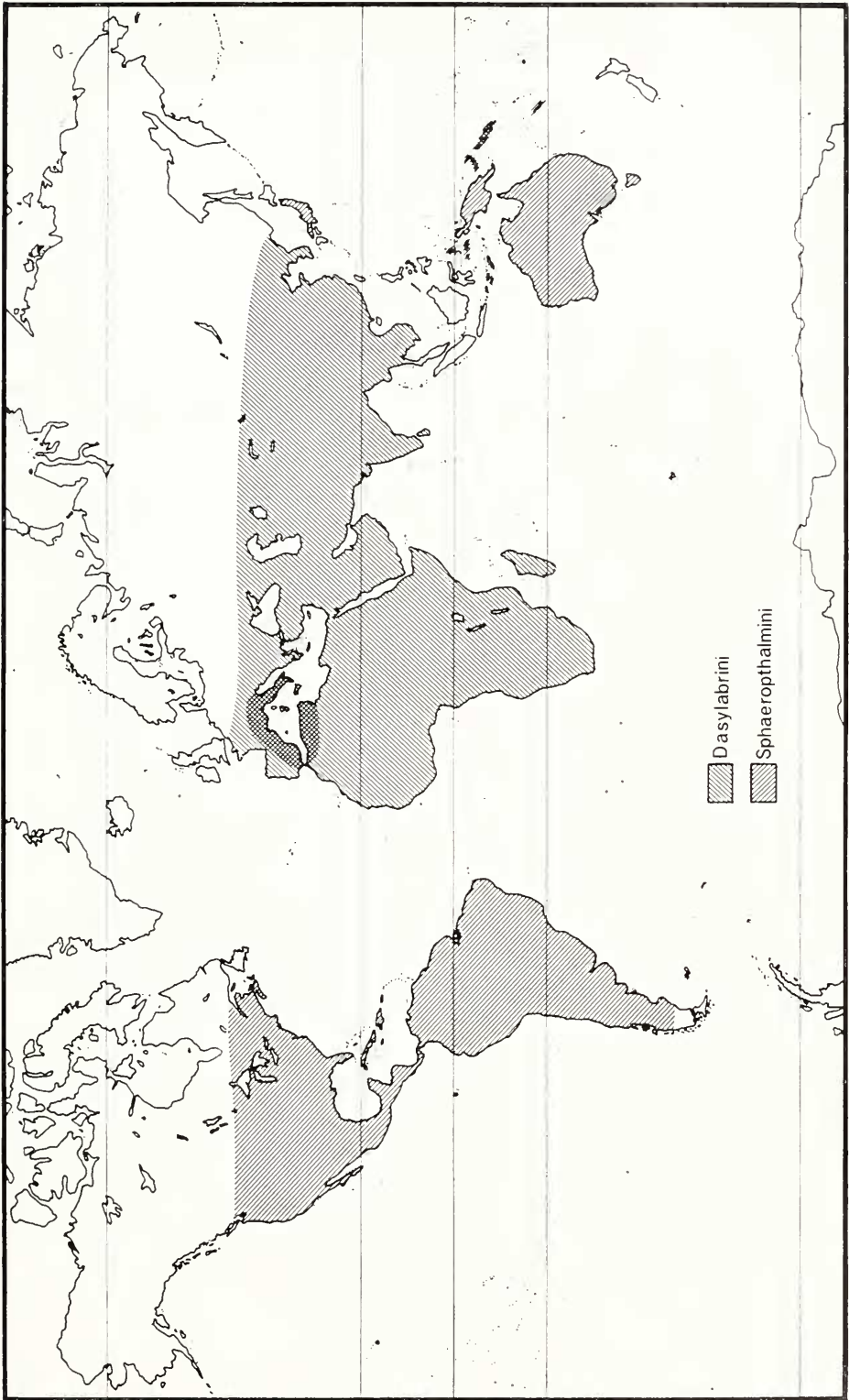


FIG. 99. Geographic distribution of both tribes of Sphaerophthalminae (Mutillidae).

tablished in South America, the Sphaerophthalmini apparently radiated extensively and rapidly, establishing two basic lines at this time (viz., Pseudomethocina and Sphaerophthalmina). Since Australia and South America were linked via Antarctica until much more recently (50 m.y. ago), most of the Australian fauna (predominantly Sphaerophthalmina, very few Pseudomethocina and Mutillini) could easily have been derived from the South American. In fact the most highly derived members of the Sphaerophthalmina seem to be various members of the "*Ephutomorpha* complex," especially those on New Guinea. (This type of progression is an important factor in establishing probable routes of dispersal; Hennig, 1966b.) Furthermore, there are various Australian species which share some highly characteristic derived features with a few South American genera (e.g., the flangelike expansions of the antennal tubercles in the females of *Scaptodactyla*), and the females of the South American (southern Chile and Argentina) genus *Neomutilla* are remarkably like some "*Ephutomorpha*" species in general facies. It may also be significant that there are many highly metallic species (often blue or green) in the Australasian region (especially New Guinea), whereas the only other metallic Sphaerophthalminae occur in the southern section of South America (e.g., females of *Neomutilla* and *Dimorphomutilla suavissima*). (Marked similarities have been found between the Australian and southern South American representatives of various insect groups—see Brundin, 1966; O'Brien, 1971.) That the introduction of mutillids into Australia by this route was probably relatively recent, is indicated by their absence in New Zealand, so that this dispersal probably occurred less than 80 m.y. ago. Furthermore, there are very few species (although at least two) on New Caledonia, which probably split from Aus-

tralia soon after the New Zealand—Antarctica separation. The North American sphaerophthalmine fauna is not as rich as that of South America and was apparently derived from it by a few introductions, probably when contact between the two continents was established relatively recently (10 m.y. ago).

The subfamily Myrmillinae (Fig. 98) is distributed across the Ethiopian, most of the Palearctic and the Oriental regions. The richest representation is in Africa with fewer genera in the peripheral areas and only two species in Madagascar. (These last are species of *Pygomilla*, and not *Ctenotilla* as was indicated by Krombein, 1972.) In some respects the Indian fauna is more similar to that of Africa than that of Europe. The genus *Squamulotilla*, for example, is present in Africa, India and farther east in the Oriental region. This may merely reflect ecological similarities, but perhaps indicates spread of this genus, at least, on to the Indian plate from Africa and subsequent dispersal from India on to Asia. The most highly derived species of *Squamulotilla* also tend to be those which occur the farthest east (e.g., *S. byblis*, with extreme development of the ventral lamella on the mesopleural ridge in the female, in the Philippines). Again, it appears that this subfamily originated in north-eastern Africa with subsequent dispersal, probably on to the Indian plate as well as more direct movement into Eurasia across the Arabian region.

The subfamily Mutillinae is worldwide in distribution, like the Sphaerophthalminae. Unlike the Sphaerophthalminae, however, this subfamily is richest in the Old World, except for the Australian region. The two tribes of Mutillinae also have essentially complementary distributions (Fig. 100). The Mutillini is entirely an Old World group except for one genus (*Timulla*), which is cosmopolitan. This genus shows signs of recent rapid specia-

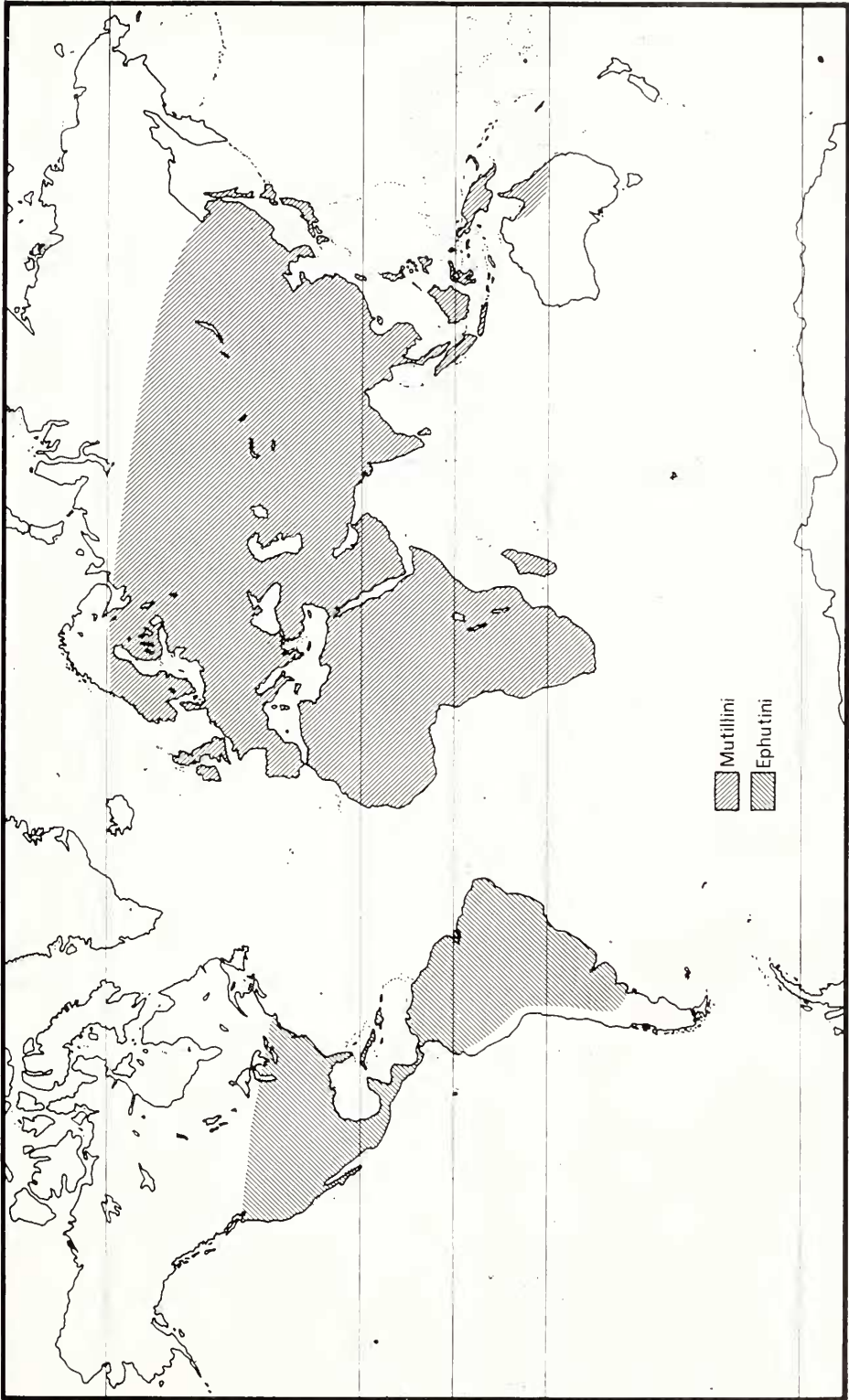


FIG. 100. Geographic distribution of both tribes of Mutillinae (Mutillidae); however, that of Mutillini excludes *Timulla* (cosmopolitan), and *Chaetotilla* and *Physctopoda* (each known from one specimen from the New World and not seen by me).

tion and so may represent a more recent introduction into the New World, perhaps via the Beringian connection. [A problem is that the species of *Timulla* with the most highly complex male genitalia (in terms of asymmetry and development of the endophallus) are African and Indian, but various species from eastern Asia and most New World species have the genitalia more nearly symmetrical (Peterson, *in litt.*). The latter would thus intuitively seem to be the less highly derived forms, which would suggest dispersal from the New World through Asia to Africa. Additional work is definitely necessary to clarify the complexities of this genus and its relatives before these problems can be solved.] The Mutillini is most richly represented in Africa, and only two species (*Odontomutilla australica* and *Timulla cooki*) extend into northern Australia. The spread into the Australasian region is thus obviously very recent and has probably occurred since the Australian and Asian plates came into contact. There are in addition two genera of Mutillini in the New World, *Chaetotilla* from Argentina and *Physetopoda* from Haiti, each known from only one specimen and not seen by me (I could not find the types in the Paris Museum), so that comment on their distribution and origin is impossible at this time.

The tribe Ephutini (Fig. 100) is entirely New World in distribution and has its greatest diversity in northern South America. It seems likely that this group also arose from a single introduction of the ancestral form from Africa to South America at about the time that these two continents separated. There was later dispersal from South America to North America, probably when these continents came into contact, but apparently no dispersal to Australia. This may have been because the ephutines seem generally to

be adapted to more tropical conditions than are many sphaerophthalmines.

It thus appears (Fig. 101) that the Mutillidae probably arose in Laurasia and diversified on the northern and eastern part of the African plate less than 180 million years ago, from where dispersal occurred on numerous occasions to India and Eurasia. Two introductions from Africa into South America probably gave rise to almost the entire New World fauna and also to most of the Australasian fauna by a few introductions across Antarctica from South America less than 80 million years ago.

Since the cladogram can be applied in this way to explain the distribution of Mutillidae in accordance with the sequences of events involved in the breakup of the continents (derived from other evidence), it appears to be supported (or at least not contradicted) by the distributional data. The likelihood that the cladogram reflects the true phylogeny of the Mutillidae is thus enhanced.

#### GENERAL CONCLUSIONS

The entire investigation of the Aculeata, including the section on the Mutillidae, has led to the proposed classification presented in Tables VI and VII. Since it has not been possible to examine each taxon with equal thoroughness, the lower levels remain to be clarified by subsequent workers in the majority of instances. Furthermore, it is quite possible that the conclusions drawn at the higher levels may in some cases prove to be unwarranted when more complete representation is obtained for various groups. Certainly, some of the relationships shown on the cladogram (such as the proximity of Scoliidæ to Vespidae and their remoteness from Tiphidae) are unexpected. These definitely warrant more intensive examination. In fact, even if the only result of this investigation is the stimulation

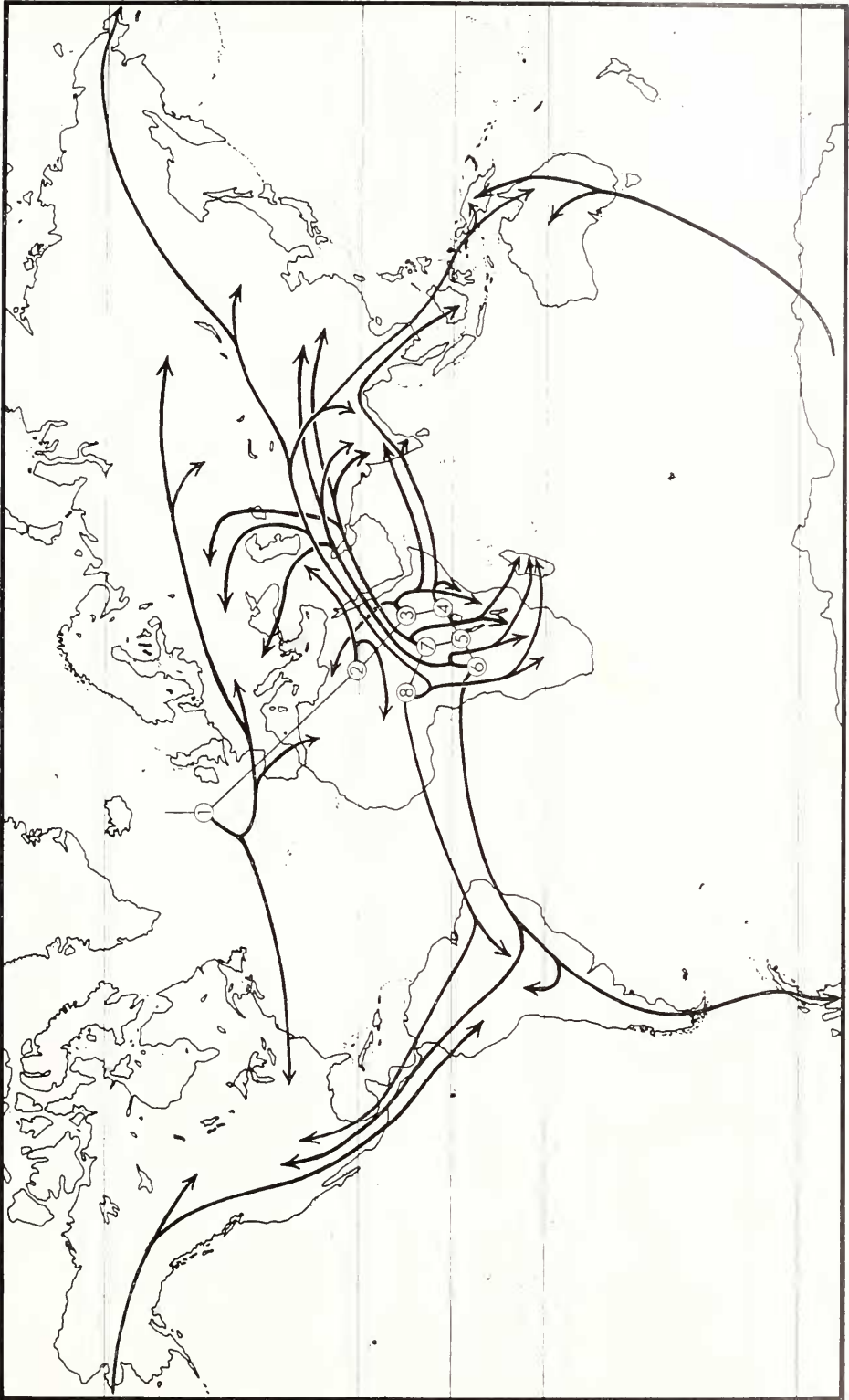


FIG. 101. Cladogram of nine taxa of Mutillidae (light straight lines and numbered nodes) and probable routes of dispersal (heavy lines) (see text for discussion).

TABLE VI. Proposed classification of the Hymenoptera Aculeata.

Superfamily	Family	Subfamily <sup>a</sup>	
BETHYLOIDEA	Plumariidae		
	Bethylidae		
	Scolebythidae		
	Cleptidae		
	Chrysididae		
	Loboscelidiidae		
	Dryinidae		
	Sclerogibbidae		
Embolemidae			
SPHECOIDEA			
	(Sphéciformes)		
		Ampulicidae	
		Sphécidae	
		Larridae	
		Mellinidae	
		Pemphredonidae	
		Astatidae	
		Philanthidae	
		Nyssonidae	
	(Apiformes)	Colletidae	
		Halictidae	
		Oxaeidae	
		Andrenidae	
		Melittidae	
		Fideliidae	
		Megachilidae	
		Anthophoridae	
		Apidae	
		VESPOIDEA	
(Vespiformes)			
	Tiphiidae		Anthoboscinae
			Thynninae
			Myzininae
			Methochinae
			Tiphiinae
			Brachycistidinae
			Fedtschenkiinae
	Sapygidae		Sapyginae
	Mutillidae <sup>b</sup>		
	Sierolomorphidae		
	Rhopalosomatidae		
	Pompilidae		
	Bradynobaenidae		Typhoctinae <sup>c</sup>
			Chyphotinae
			Apterogyninae
		Bradynobaeninae	
	Scoliidae		
	Masaridae		
	Eumenidae		
	Vespidae		
(Formiciformes)	Formicidae		

<sup>a</sup> Subfamilies indicated only for taxa previously considered to comprise the tiphoid-mutilloid group, and the Sapygidae.

<sup>b</sup> For details of subfamily divisions see Table VII.

<sup>c</sup> Comprises two tribes, Eotillini and Typhoctini.

TABLE VII. Proposed classification of the Mutillidae.

Subfamily	Tribe	Subtribe
Myrmosinae		
Pseudophotopsidinae		
Ticoplinae		
Rhopalomutillinae		
Sphaerophthalminae	Dasyabrini	
	Sphaerophthalmini	Pseudomethocina Sphaerophthalmina
Myrmillinae		
Mutillinae	Mutillini	Mutillina
	Ephutini	Smicromyrmina

of critical studies which may refute the conclusions presented here, then it will have accomplished its purpose.

Those conclusions which are most at variance with the current ideas on the classification of the Hymenoptera Aculeata, may be summarized as follows:

a) The Aculeata should be considered as comprising only three superfamilies (Bethyloidea, Vespoidea, Sphecoidea) as opposed to the previously commonly accepted seven.

b) The Scolebythidae and Plumariidae should be included with seven other families in the Bethyloidea.

c) The Vespoidea should be divided into two informal groups, the Vespiformes (with 11 families) and the Formiciformes (1 family).

d) The Sphecoidea should be divided into two informal groups, the Spheciiformes (with 8 families) and the Apiiformes (9 families).

e) The Myrmosinae and Bradynobaeninae should be removed from the Tiphidae.

f) The "Eotillinae," "Typhoctinae" and "Apterogyninae" ("Chyphotini" and "Apterogynini") should be removed from the Mutillidae.

g) The family Bradynobaenidae should be recognized as comprising the subfamilies Typhoctinae, Chyphotinae, Apterogyninae and Bradynobaeninae.

h) The subfamily Typhoctinae should

be recognized as comprising two tribes, the Typhoctini and Eotillini.

i) The family Mutillidae should be divided into seven subfamilies, the Myrmosinae, Pseudophotopsidinae, Ticoplinae, Rhopalomutillinae, Myrmillinae, Mutillinae and Sphaerophthalminae.

j) The subfamily Mutillinae should be recognized as comprising two tribes, the Mutillini and Ephutini.

k) The tribe Mutillini should be recognized to comprise two subtribes, the Mutillina and Smicromyrmina.

l) The subfamily Sphaerophthalminae should be divided into two tribes, the Dasyabrini and Sphaerophthalmini.

m) The tribe Sphaerophthalmini should be recognized as comprising two subtribes, the Pseudomethocina and Sphaerophthalmina.

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